UNIVERSIDADE FEDERAL DO PARANÁ

ANA CAROLINE OLIVEIRA VASCONCELOS

PHYLOGENY OF PTEROCALLINI AND TAXONOMY OF THE STALK-EYED FLY *PLAGIOCEPHALUS* WIEDEMANN (DIPTERA, ULIDIIDAE)

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PHYLOGENY OF PTEROCALLINI AND TAXONOMY OF THE STALK-EYED FLY *PLAGIOCEPHALUS* WIEDEMANN (DIPTERA, ULIDIIDAE)

Dissertação apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Entomologia), Setor Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de mestre.

Orientador: Dr. Claudio J. B. de Carvalho, Universidade Federal do Paraná (UFPR)
Coorientadora: Dra. Lisiane Dilli Wendt, Universidade Federal do Paraná (UFPR)

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RESUMO

Pterocallini é uma tribo Neotropical de Ulidiidae (Diptera) e também uma das maiores da família, com mais de 130 espécies descritas em 27 gêneros. Além das características morfológicas presentes em Ulidiidae, os Pterocallini são reconhecidos pela asa com variados padrões de manchas escuras. Geralmente, as espécies da tribo também apresentam dimorfismo sexual na asa ou na forma da cabeça. O gênero com um dos dimorfismos sexuais mais peculiares dentre os Pterocallini é *Plagiocephalus*, cujo os machos possuem os olhos extremamente pedunculados. Tanto *Plagiocephalus*, quanto os outros gêneros da tribo, nunca foram amostrados em filogenias, assim, a monofilia e os relacionamentos filogenéticos entre eles nunca foram investigados. Os objetivos do presente trabalho são propor a primeira hipótese de relacionamento filogenético para Pterocallini e atualizar o conhecimento taxonômico de *Plagiocephalus*. Vinte um gêneros da tribo foram amostrados em uma análise filogenética com dados morfológicos. Uma matriz com 58 táxons terminais e 92 caracteres foi construída, e uma análise de parcimônia foi realizada utilizando pesagem igual e pesagem implícita dos caracteres. A árvore gerada pela análise com constantes de concavidade igual à 10–13 produziu uma árvore mais parcimoniosa e corroborou vários agrupamentos monofiléticos internos à tribo. A monofilia dos gêneros *Aciuroides*, *Lathrostigma*, *Neomyennis*, *Plagiocephalus*, *Pseudopterocalla*, *Pterocalla*, *Rhyparella*, *Terpnomyia* e *Xanthacrona* pôde ser suportada. Entretanto, a análise não corroborou a monofilia de *Apterocerina*, *Megalaemyia*, *Paragorgopis* e *Pterocerina*. Uma revisão taxonômica destes gêneros merece ser realizada no futuro para se estabelecer os limites taxonômicos destes táxons. Caracteres da terminália foram adicionados à descrição de *Plagiocephalus* e mapas de distribuição geográfica com novos registros de ocorrência foram construídos para as espécies do gênero.

Palavras-chave: morfologia, Neotrópico, sistemática, ulidídeos.

ABSTRACT

Pterocallini is a Neotropical tribe of Ulidiidae (Diptera) and also one of the largest tribes of the family, with more than 130 species described in 27 genera. In addition to the morphological characters present in Ulidiidae, the Pterocallini species are recognized by the varied patterns of dark spots on the wing. Generally, the species of the tribe also exhibit sexual dimorphism in the wing or in the shape of the head. The genus with one of the most peculiar sexual dimorphisms among the Pterocallini is *Plagiocephalus*, in which the males present eyes extremely stalked. As *Plagiocephalus*, the other genera of the tribe have never been sampled in phylogenies, so the monophyly and the phylogenetic relationships among them have never been investigated. The objectives of the present work are to propose the first hypothesis of phylogenetic relationship for Pterocallini and to update the taxonomic knowledge of *Plagiocephalus*. Twenty-one genera of the tribe were sampled in a phylogenetic analysis with morphological data. A matrix with 58 terminal taxa and 92 characters was constructed, and a parsimony analysis was performed under equal weighting and implied weighting of the characters. The analysis under constants of concavity equal to 10–13 produced one most parsimonious tree and corroborated the monophyly of several groupings internal to the tribe. The monophyly of the genera *Aciuroides*, *Lathrostigma*, *Neomyennis*, *Plagiocephalus*, *Pseudopterocalla*, *Pterocalla*, *Rhyparella*, *Terpnomyia* and *Xanthacrona* could be supported. However, the analysis did not corroborate the monophyly of *Apterocerina*, *Megalaemyia*, *Paragorgopis* and *Pterocerina*. A taxonomic revision of these genera deserves to be undertaken in the future for establishing the taxonomic limits of these taxa. Characters of the terminalia of *Plagiocephalus* were added in the description and geographic distribution maps with new records were constructed for the species of the genus.

Key words: morphology, Neotropics, systematics, ulidiids.

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

SUMMARY

INTRODUCTION

The superfamily Tephritoidea

Tephritoidea are an acalyptrate group of flies including over 7300 described species (Han & Ro 2016). The monophyly of the superfamily is supported by four morphological synapomorphies of the abdomen: male tergum 6 strongly reduced or absent, medial surstylus bearing toothlike presinsetae, female sternites with anterior apodemes, and female tergosternum 7 with the anterior portion forming an oviscape and the posterior portion forming two longitudinal taeniae (Griffiths 1972; McAlpine 1989; Korneyev 1999). Based on these synapomorphies, Korneyev (1999) considered that Tephritoidea are composed of eight families: Lonchaeidae, Pallopteridae, Platystomatidae, Piophilidae, Pyrgotidae, Richardiidae, Tephritidae and Ulidiidae. Recently, Ctenostylidae and Eurygnathomyiidae, which had an unstable classification, were also recovered as part of the superfamily (Han & Ro 2016). Additionally to these families, Papp (2011) proposed Circumphallidae, a new family based on a single species, as part of Tephritoidea. However, the positioning of Circumphallidae in the superfamily has not been tested through phylogenies.

The relationships among the families of Tephritoidea have been investigated by morphological analysis over the last 60 years (Hennig 1958, 1971, 1973; Griffiths 1972; McAlpine 1989; Korneyev 1999). Recently, there were also attempts to hypothesize the relationship among the families of Tephritoidea using molecular data (Han et al. 2002; Han & Ro 2005, 2016). However, it is still controversial the number of families that belong to the superfamily and the relationship among them (Korneyev 1999; Han et al. 2002; Han & Ro 2005, 2016; Wiegmann et al. 2011). The position of Ulidiidae in phylogenies of Tephritoidea has also not been solved. However, Ulidiidae have been recovered in mostly phylogenies proposed for the superfamily as the sister group of (Platystomatidae (Tephritidae, Ctenostylidae, Pyrgotidae)), with the relationship among Tephritidae, Ctenostylidae and Pyrgotidae not being consensus (McAlpine 1989; Korneyev 1999; Han & Ro 2005, 2016).

Ulidiidae and the tribe Pterocallini

Ulidiidae Macquart, 1835 are the third largest family of Tephritoidea, after Tephritidae and Platystomatidae, with about 700 described species (Galinskaya et al. 2014; Kameneva & Korneyev 2010). Ulidiids are broadly distributed in the New World, in a lesser magnitude in the Palearctics, and have a few species occurring in Africa, Asia and Oceania (Kameneva 2012). Some species of the family are associated with monocotyledons, sugar beet and cherries, being important agricultural pests in the Americas. Others are associated with pines, cactus or rotting plant matter. Adults are usually attracted to decaying matter, such as carrion, hydrolyzed protein and compost, and mostly known larvae of the family are saprophagous (Allen & Foote 1967; Kameneva & Korneyev 2010).

Ulidiidae went through many classifications and nomenclatural changes throughout their history. Loew (1868) was the first author to propose a classification for the family, as Ortalidae, recognizing seven groups: Cephalina, Ortalina, Platystomina, Pterocallina, Pyrgotina, Richardiina and Ulidiina. Later, Hendel (1909a, 1909b, 1910a, 1910b, 1911, 1914) classified Ortalinae, Pterocallinae and Ulidiinae as subfamilies of Muscaridae, and Hendel (1928) considered them as separated families. The name Ortalidae, based on *Ortalis* Fállen, 1810, was found already in use in Aves (junior homonymy of *Ortalis* Merrem, 1786) (Aldrich 1932). Then, a new family name, Otitidae Aldrich, 1932, was proposed to replace Ortalidae. Curran (1934a, 1934b) united Otitidae, Ulidiidae, Pterocallidae, Platystomatidae and Richardiidae into a unique family, Otitidae. Hennig (1939, 1940, 1973) distinguished Otitidae (including Pterocallinae) from Ulidiidae, since a synapomorphy to support the union of both groups was not found. Steyskal (1961, 1965, 1968, 1977, 1987) excluded Platystomatinae and Richardiinae from Otitidae, treating them as separated families. Kameneva and Korneyev (1994) demonstrated that the senior name that unites Otitidae and Ulidiidae into a single family is Ulidiidae Macquart, 1835 rather than Otitidae Aldrich, 1932. Finally, the name Ulidiidae started to be accepted as the only valid name for the family.

Ulidiids are very diverse in color and shapes, and most species have dark bands or spots on the wings. They possess most of the characters of Tephritoidea, as tibiae without a row of setae, surstylus bearing toothlike presinsetae, phallus long, coiled and stored on

the ventral side of the abdomen, and female tergosternum 7 and 8 forming a well developed telescopic ovipositor (Kameneva & Korneyev 2010). Ulidiidae together with Tephritidae, Platystomatidae and Pyrgotidae form a monophyletic group within Tephritoidea, which was called by Korneyev (1999) as Higher Tephritoidea. The synapomorphies that support the moophyly of the clade are the completely reduced spiracles 6 and 7, and setae on the abdominal sternite 6 of males (Korneyev 1999; Kameneva & Korneyev 2010). Monophyly of Ulidiidae is supported by the absence of presutural supra-alar setae and anepimeral setae and setulae (Kameneva & Korneyev 1994, 2006, 2010).

Kameneva and Korneyev (1994, 2006) proposed the newest suprageneric classification of the family. Ulidiidae are subdivided into two subfamilies, Ulidiinae and Otitinae. Ulidiinae is composed of four tribes: Lipsanini Enderlein, 1938, Pterocallini Loew, 1868, both widely distributed in the Neotropical region, Seiopterini Kameneva & Korneyev, 1994, with Holarctic distribution, and Ulidiini Macquart, 1835, with the majority of genera recorded in the Eastern Hemisphere. Otitinae include three tribes: Cephaliini Schiner, 1864, Myennidini Kameneva & Korneyev, 2006 and Otitini Aldrich, 1932, with mostly genera occurring in the Holarctic region (Kameneva & Korneyev 2010).

Pterocallini were often considered as a subfamily, Pterocallinae, (Hendel 1909a, 1909b, 1910a, 1910b, 1914) or as a family, Pterocalllidae (Hendel 1916, 1928, 1936). Hendel (1909a, 1914) described about half of the genera of the tribe within Pterocallinae, a subfamily of Muscaridae. Hendel (1916) proposed a family rank for Pterocallini, and Hennig (1939) synonymized Pterocallidae with Otitidae. Steyskal (1961, 1963) treated Ulidiidae and Pterocallidae as subfamilies of Otitidae, and later, the author (Steyskal 1968, 1982) considered Pterocallini a tribe of Otitinae, justifying that they are "apomorphic members" of this subfamily. Kameneva and Korneyev (1994) followed the classification of Steyskal (1968, 1982) and considered Pterocallini a tribe of Otitinae. Thereafter, Kameneva and Korneyev (2006), because of the absence of apodemes in the sternites of females, reclassified Pterocallini into the subfamily Ulidiinae.

The genera composing Pterocallini are recognized by the coloration usually brown, most members sexually dimorphic, with the pterostigma enlarged in some males,

vein R_{2+3} usually sinuous, male terminalia with part of the ejaculatory apodeme adjoining the sperm sac extremely elongate, phallus bare or microsetulose, and female terminalia with three spherical spermathecae with smooth surface (Kameneva & Korneyev 2006). Pterocallini and Lipsanini are the largest tribes of Ulidiidae in number of genera. Accordingly with the classification of Kameneva and Korneyev (2006), Pterocallini are composed of 24 Neotropical genera: *Aciuroides* Hendel, 1914, *Bothrometopa* Hendel, 1909, *Chondrometopum* Hendel, 1909, *Coscinum* Hendel, 1909, *Cymatosus* Enderlein, 1912, *Cyrtomostoma* Hendel, 1909, *Dasymetopa* Loew, 1868, *Elapata* Hendel, 1909, *Goniaeola* Hendel, 1909, *Idanophana* Hering, 1938, *Megalaemyia* Hendel, 1909, *Micropterocerus* Hendel, 1914, *Neomyennis* Hendel, 1914, *Ophthalmoptera* Hendel, 1909, *Paragorgopis* Giglio-Tos, 1893, *Plagiocephalus* Wiedemann, 1830, *Pterocalla* Rondani, 1848 (including *Pseudopterocalla* Hendel, 1909), *Pterocerina* Hendel, 1909, *Rhyparella* Hendel, 1909, *Sympaectria* Hendel 1909, *Terpnomyennis* Kameneva, 2004, *Terpnomyia* Hendel, 1909, *Tetrapleura* Schiner, 1868 and *Xanthacrona* Wulp, 1899.

Some taxonomical changes within Pterocallini have occurred since the classification proposed by Kameneva and Korneyev (2006). Kameneva and Korneyev (2010) synonymized *Sympaectria* with *Pterocerina*, and Kameneva (2012) synonymized *Idanophana* with *Aciuroides*. According to Kameneva (2012), *Micropterocerus* is also probably going to be synonymized with either *Pterocerina* or *Tetrapleura*, since the genus was established from males of sexually dimorphic species. Some authors treated *Pseudopterocalla* as a subgenus of *Pterocalla* (Hendel 1909b, Steyskal 1982), and Steyskal (1968) considered *Parophthalmoptera* Hendel, 1914 as a subgenus of *Ophthalmoptera*, but Kameneva and Korneyev (2010) maintained then as separated genera. Moreover, other works (Kameneva & Korneyev 2010, Kameneva 2012) considered *Apterocerina* Hendel, 1914, *Lathrostigma* Enderlein, 1921 and *Neoacanthoneura* Hendel, 1914 as genera of Pterocallini. In total, Pterocallini have more than 130 described species in 27 recognized genera: *Aciuroides*, *Apterocerina*, *Bothrometopa*, *Chondrometopum*, *Coscinum*, *Cymatosus*, *Cyrtomostoma*, *Dasymetopa*, *Elapata*, *Goniaeola*, *Lathrostigma*, *Megalaemyia*, *Micropterocerus*, *Neoacanthoneura*, *Neomyennis*, *Ophthalmoptera*, *Paragorgopis*, *Parophthalmoptera, Plagiocephalus*, *Pseudopterocalla*, *Pterocalla*, *Pterocerina*, *Rhyparella*, *Terpnomyennis*, *Terpnomyia*,

Tetrapleura and *Xanthacrona*.

Phylogenetic analyses at any level of Ulidiidae are scarce. Kameneva and Korneyev (1994, 2006), respectively, proposed a phylogenetic hypothesis based on morphological characters for nine genera of Ulidiidae and for the tribe Myennidini. Galinskaya et al. (2014), utilizing morphology and the fragment of the DNA barcoding, presented a phylogeny of the Palearctic ulidiids, which are mainly genera of the subfamily Otitinae. However, Galinskaya et al. (2014) utilized in their molecular analysis only mitochondrial DNA, which is not suitable for solving suprageneric relationships. Also, the authors did not make the methodology and the characters of the morphological phylogenetic analysis explicit. Until now, there is no comprehensive hypothesis of internal phylogenetic relationships for Ulidiidae. Because of the absence of phylogenetic studies on the family, the classification of the tribes and genera of Ulidiidae is not based on a phylogenetic perspective. The taxonomical and phylogenetic knowledge of Pterocallini is even deficient. The tribe has not been sampled in any analysis of the family and most of their genera have not been taxonomically revised.

The genus *Plagiocephalus* Wiedemann

Plagiocephalus Wiedemann, 1830 is a very peculiar genus of Pterocallini, in which the males of all three species, *P. lobularis* (Wiedemann, 1830), *P. latifrons* (Hendel, 1909) and *P. intermedius* Kameneva, 2004, present the eyes stalked. The species of *Plagiocephalus* are characterized mainly by the transverse head in both sexes, in males sometimes reaching five times the length of the body (Grimald & Engel 2005), body brownish with grey and yellow microtrichia in bands and spots on the thorax and abdomen, wing with pattern of dark bands, vein R_1 with setae on the apical half, vein R_{2+3} almost straight and cell cup with very short posteroalpical lobe (Kameneva 2004b).

Wiedemann (1830a) described the first species of the genus, *Plagiocephalus lobularis*, originally combined with *Achias* (Platystomatidae), another genus of stalk-eyed fly. In another work in the same year, Wiedemann (1830b) described the genus *Plagiocephalus* and considered *A. lobularis* a species of this genus. Blanchard (1938a), from a male specimen, described *Paragoniaeola tanycephala*, but Aczél (1951) synonymized it with *P. lobularis*. Blanchard (1938b), now from female specimens,

described *Eupterocerina conjucta*, which was synonymized with *P. lobularis* by Steyskal (1968). *Ophryoterpnomyia zikani* Capoor (1954) was also synonymized with *P. lobularis* by Steyskal (1963).

Hendel (1909a) described the second species of the genus, *P. latifrons*, originally combined with the genus *Terpnomyia*. Hendel (1936), because of differences in the head from other species of *Terpnomyia*, created a new genus, *Ophryoterpnomyia*, to allocate *T. latifrons*. *Ophryoterpnomyia* was synonymized with *Plagiocephalus* by Carrera (1950). Frey (1926) described *Stylophthalmyia fascipennis*, which was synonymized by Steyskal (1963) with *P. latifrons*. Another synomym of *P. latifrons*, *Willineria orfilai*, described by Blanchard (1951), was later synonymized with that species by Steyskal (1964).

Kameneva (2004b) described *P. intermedius*, the last known species of *Plagiocephalus*. Carrera (1950), Steyskal (1963) and Kameneva (2004b) revised the genus, and only Steyskal (1963) presented an illustration of the male terminalia of one of the species, *P. latifrons*. *Plagiocephalus*, as the rest of the Pterocallini, has never been studied in a phylogenetic context.

OBJECTIVES

The main objective of this work is to present the first phylogeny of Pterocallini. The specific objectives are the following:

1. To propose a hypothesis of relationship among the genera of Pterocallini.
2. To test the monophyly of some of the genera of Pterocallini.
3. To revise the *Plagiocephalus* species providing characters of the terminalia and maps of geographical distribution.

MATERIAL AND METHODS

Examined material

The material analyzed in this work was prevenient from the following institutions with the respective curators (the acronyms marked with an asterisk are institutions that provided photographs of the types):

CEUA: Colección Entomológica, Universidad de Antioquia, Medellín, Colombia (Marta Wolff);

CZMA: Coleção Zoológica do Maranhão, Universidade Estadual do Maranhão, Caxias, Maranhão, Brazil (Francisco Limeira-de-Oliveira);

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INTA*: Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina;

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MNRJ: Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Márcia S. Couri);

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NHMUK: National History Museum of London, London, England (Daniel Whitmore);

NHMW*: Naturhistorisches Museum Wien, Vienna, Austria (Peter Sehnal);

USNM: United States National Museum of Natural History, Department of Entomology, Washington, District of Columbia, United States (Allen L. Norrbom);

ZMHB*: Museum für Naturkunde der Humbolt-Universität zu Berlin, Berlin, Germany

(Michael Ohl);
ZMUC*: Zoological Museum University of Copenhagen, Copenhagen, Denmark (Thomas Pape).

Visits to search for material of *Plagiocephalus* were made in INPA, UFBA (Coleção de Insetos Aquáticos do Museu de Zoologia da Universidade Federal da Bahia, Salvador, Bahia, Brazil (Adolfo Calor)), MZFS (Coleção Entomológica Prof. Johann Becker do Museu de Zoologia da Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil (Freddy Bravo)), MNRJ, MZSP and LACM. Other institutions from Brazil and from other countries were contacted to request a loan of specimens, but there was no success for the lack of material of *Plagiocephalus*.

The type material of *Plagiocephalus* and other genera was only examined by photos. The description of the labels of the type material of the species of *Plagiocephalus* was obtained from Kameneva (2004), and listed utilizing quotation marks for each label attached to the specimens. The list of analyzed material of *Plagiocephalus* was presented according to the following sequence: country, state, locality, coordinates, date, collector, number and sexes of the specimens, and collection.

Collecting

Specimens of *Plagiocephalus* and other genera of Ulidiidae were collected with the objective of adding them to the phylogenetic analysis and extracting DNA in a future research. Collectings were made in the Mata Viva, Centro Politécnico, Universidade Federal do Paraná, Curitiba, Paraná, Brazil and in the Estação Experimental ZF-2, Manaus, Amazonas, Brazil. The collectings made in the Mata Viva were conducted between December 2016 and April 2017, and in the Estação Experimental ZF-2 from 17 to 21, August 2017. McPhail traps were installed with hydrolyzed protein 5%, an attractive compost utilized for collecting pest species of *Anastrepha* (Tephritidae) (Ortega & Cabrera 1996). Five traps were installed in the Mata Viva, where they were inspected within an interval of about four days. In the Estação Experimental ZF-2, 26 traps were installed and kept in the field for five days.

Identification of the material

The specimens analyzed were identified by original descriptions, identification keys of genus or species of Ulidiidae (Hendel 1909a, 1909b; Steyskal 1982; Kameneva & Korneyev 2010) and by comparison with photographs of type specimens.

Terminology

The external terminology (Figs. 1A–E) followed Cumming and Wood (2010), with the exception of the wing pattern (Fig. 1C), which followed White et al. (1999). Male terminalia structures (Figs. 2A–D) followed White et al. (1999), and female terminalia structures (Figs. 2E–F) followed Norrbom & Kim (1988).

Preparation of the terminalia

For observation of the male and female terminalias the entire abdomen of specimens was dissected with fine scissors. It was used two procedures for the preparation of the terminalia. In the first, the abdomen of some of the specimens was heated with acid lactic 85% for clarification. The time for each abdomen to clarify varied from 15 to 20 minutes depending on the size of the specimen. In the second procedure, the abdomen of other specimens was left in KOH 10% overnight, and after that, they were neutralized with acetic acid for 30 minutes. After clarification, the abdomen was washed with alcohol 70% and conserved in glycerin. The terminalias were mounted in slides with glycerinated gelatin for photographs. Posteriorly to the examination, photographing and illustration, the terminalias were stored in a small tube attached to the pin of the belonged specimen.

Observation of the specimens and construction of the plates

Specimens were examined under a Zeiss Stemi DV4 stereoscopic microscope. Photographs of the specimens were taken with Auto-Montage Imaging System® Leica DFC 500 in the Taxonline (UFPR). Some of the photographs were taken with the photographing digital microscope of the Entomology Collection of the Natural History Museum of Los Angeles County. Drawings were made with microscope Zeiss Standard 20 coupled with a lucid camera. Photographs were processed on Adobe Photoshop CC (https://www.adobe.com/products/photoshop/free-trial-download.html) and drawings were vectored on Adobe Illustrator CC (https://www.adobe.com/products/illustrator/free-

trial-download.html).

Phylogenetic analysis

Taxon sampling

Twenty-one genera were sampled out of the 27 current genera in Pterocallini (Table 1). The sampling of species sought to include the type species and at least two species of each genus (Appendix 1). *Apterocerina*, *Chondrometopum*, *Dasymetopa*, *Neoacanthoneura*, *Paragorgopis* and *Pterocerina* did not have the type species included in the analysis. Only *Apterocerina*, *Chondrometopum*, *Cymatosus*, *Dasymetopa*, *Megalaemyia*, *Neoacanthoneura*, *Neomyennis*, *Paragorgopis*, *Pterocalla* and *Pterocerina* did not have all the species added in the phylogenetic analysis. Two species of Lipsanini (Ulidiinae) and two species of Cephallini (Otitinae) were used as outgroups of the analysis (Appendix 1). The monophyly of Pterocallini could not be tested due to the lack of material of the family to compose the analysis.

Construction of the characters

Due to the deficiency of phylogenetic analysis of Ulidiidae and lack of known informative characters, most characters in this work were proposed based on the direct observation of specimens. Some characters used in the phylogeny of Richardiinae (Richardiidae) (Wendt 2012) were utilized in this work (commented below the character when it is the case). The construction of the characters was based on Sereno (2007) and Brazeau (2011). Contigent coding was prioritized for the construction of the characters (Brazeau 2011). The matrix was built in the program Mesquite 3.2 (Maddison & Maddison 2011). The symbol "?" was used for taxa with unknown character state and the symbol "-" for inapplicable character (Appendix 2).

Analysis

The parsimony analysis was undertaken on the software TNT (Goloboff & Catalano 2016). Characters with multiple states were treated as unordered. The analysis was performed under equal weighting (EW) and implied weighting (IW) (Goloboff 1993). Implied weighting was carried out using values of *k* (constant of concavity) from

one to 30. Different values for the constant of concavity were used to determine the preferred tree through an "analysis of sensibility" (Wheeler 1995; Goloboff et al. 2008). The constant of concavity penalizes homoplastic characters favoring characters with better phylogenetic congruence. The concavity and weighting of homoplasy become less intense the higher is the value of k (Goloboff 1993).

The analysis was made using *Traditional Search* with the algorithm TBR (*tree bisection and reconnection*). The parameters used in the *Traditional Search* were random seed 0, 1000 replications and 100 trees salved. The analyses were also ran using the algorithms of *New Technology* (*Sectorial Search*, *Ratchet*, *Drift* and *Tree Fusing*) in the default mode of the program and, also, changing the parameters of the *Ratchet* search for 20 total number of interactions, *Drift* search for 20 total cycles and *Tree Fusing* for 5 rounds. The algorithms of *New Technology* were used with random seed 0, 1000 initial sequences, 100 salved trees, and with the minimum tree length found 50 times. Because of the time spending on analysis with *New Technology* (the search on default mode examined more than 140 billions of rearrangements in approximately 3 hours) and no difference in topology or statistical parameters values were found among the resulted trees and the trees originated by the analysis using the TBR algorithm, it was chose the TBR to perform the analysis with different values of *k*. Nodes with a minimum length of zero were collapsed in all trees and all the analysis were carried out with a space of 99.999 trees in memory.

The optimization of the characters was made in the software Winclada 1.61 (Nixon 2002) through unambiguous optimization. The branches support was calculated by the Relative Bremer Support in the software TNT, with stored suboptimal trees with length up to 15 additional steps. The Relative Bremer Support indicates the proportion between favorable and contrary evidence to the existence of a clade (Goloboff & Farris 2001). The tree rooting was established between Cephallini and the lasting genera, since Cephallini is classified into the other subfamily of Ulididae (Otitinae) and, possibly, is more distantly related to Pterocallini than Lipsanini (Kameneva & Korneyev 2006). The trees were edited on Adobe Illustrator CC.

Descriptions

For the taxonomical revision of *Plagiocephalus* it was made a general description of the genus and added new characters in the diagnoses of the species, which were based on Kameneva (2004b). Since an efficient key for the species has already been given in Kameneva (2004b), making a new key was uneeded. Because I did not have access to any male of *P. intermedius*, the male terminalia of this species could not be described.

Maps of geographical distribution

The geographical coordinates were obtained from the material of *Plagiocephalus* listed in the literature and from the specimens analyzed. In cases that the coordinates were not specified in the label, they were searched from the locality data of the label on Google Earth Pro (https://earth.google.com/download-earth.html). For the construction of the maps, only the localities that could provide unambiguous coordinates were used. The maps were made on QGIS 2.18.14 using a Latin America political shape and a physical raster from the Esri plugin installed on the QGIS.

RESULTS

List of characters

The matrix was composed of 58 terminals, in which four of them were outgroup. Ninety-two characters were built based on the external morphology of adults males and females, wherein 21 are of the head, 14 of the thorax, 20 of the wing, two of the legs, five of the abdomen, 11 of the female terminalia and 19 of the male terminalia. Subsequent to each character, the number of steps (L), the consistency (IC) and retention (IR) indexes of the preferred tree were included. Some characters were commented and some states were photographed (Figs. 3–10).

Head (Figs. 3A–I, 4A–J)

0. Male head, frontal view, shape (L = 4; IC = 50; IR = 60):

(0) rounded (width and length of similar size, at most 1.5 wider than high) (Figs. 3A, D–F, H, I);

(1) transverse (between 1.8 and 2.5 wider than high) (Fig. 3G);

(2) extremely transverse (more than 2.7 wider than high) (Figs. 20A, D).

In *Paragorgopsis incus* Kameneva, *Paragorgopsis* sp. and *Plagiocephalus*, the males present the head wider than females. In *Bothrometopa*, males and females present transverse head. Although it was analyzed only the female with transverse head of a undescribed species of *Chondrometopum*, it was assumed that the male also presents transverse head, since it is usual for the species of the genus both sexes present the same shape of the head (Kameneva 2004a). The width of the head was measured above the antennae from eye to eye, and the height from the vertex to the line between face and clypeus.

1. Ocellar triangle, shape (L = 4; IC = 25; IR = 83):

(0) equilateral triangle (Figs. 4B–D);

(1) isosceles triangle (Fig. 4A).

In the state (0), the ocelli are almost equally distanced from each other. In the state (1), the anterior ocellus is more distant from the posterior ocelli than the posterior ocelli between each other.

Wendt (2012) used this character in the phylogenetic analysis of Richardiinae (Richardiidae).

2. Ocellar triangle, position (L = 4; IC = 25; IR = 83):
(0) almost aligned with the inner vertical setae (Figs. 4B, C, D);
(1) anterior to the inner vertical setae (Fig. 4A).

Wendt (2012) used this character in the phylogenetic analysis of Richardiinae (Richardiidae).

3. Ocellar setae, length in relation to the postocellar setae (L = 12; IC = 16; IR = 54):
(0) distinctly shorter;
(1) about the same size;
(2) distinctly longer (Fig. 4E).

4. Inner vertical setae, length in relation to the outer vertical setae (L = 8; IC = 12; IR = 72):
(0) distinctly longer (Figs. 3A, D, E);
(1) about the same size (Figs. 3B, C, G).

In the state (0), the inner vertical setae are about 1.5 times the length of the outer vertical setae.

5. Orbital lower setae, size in relation to the orbital upper setae (L = 7; IC = 14; IR = 62):
(0) weaker (Figs. 4F, H);
(1) as strong as the orbital upper setae (Fig. 4E).

6. Orbital lower setae, position in relation to the lunule and orbital upper setae (L = 4; IC = 25; IR = 85):
(0) middle distance between orbital upper setae and lunule (Fig. 4E);
(1) closer to the orbital upper setae (Figs. 4F, H).

Kameneva (2012) commented that the orbital lower setae at middle of the frons (state (0)) is one of the shared characters of the group that includes *Aciuroides*, *Apterocerina*, *Coscinum* (not included in the analysis), *Cyrtomostoma*, *Elapata* (not

included in the analysis), *Lathrostigma*, *Micropterocerus* (not included in the analysis), *Pterocerina* and *Tetrapleura*.

7. Frons, texture (L = 2; IC = 100; IR = 100):

(0) smooth (Figs. 3A, B, D–H);

(1) granulated (Fig. 3C);

(2) foveolated (Fig. 3I).

8. Frons, setae (L = 2; IC = 50; IR = 75):

(0) present;

(1) absent.

Setae on the frons are absent in most of the Pterocallini. *Neoacanthoneura* in the only genus that most of the species have setae on the frons.

9. Frons, setae, number (L = 1; IC = 100; IR = 100):

(0) two;

(1) three;

(-) not applicable.

10. Eyes, lateral view, shape (L = 11; IC = 27; IR = 63):

(0) oval (higher than wide) (Figs. 4E, H);

(1) rounded (similar height and width);

(2) squared (similar height and width with almost straight bottom margin);

(3) wide (wider than high) (Fig. 4F).

11. Gena, height in relation to the height of the eye (L = 12; IC = 16; IR = 50):

(0) very short, less than 1/4 the height of the eye (Figs. 4E, H);

(1) short, between 1/4 and 1/3 the height of the eye (Fig. 4F);

(2) high, more than half the height of the eye (Fig. 4G).

12. Parafacialia, pattern of coloration (L = 1; IC = 100; IR = 100):

(0) transversal spot;

(1) without differentiated coloration.

The transversal spot in the parafacialia is present only in the females of *Plagiocephalus*.

13. Lunule, frontal view, expansion above the antennae (L = 3; IC = 66; IR = 66):

(0) non-expanded (Figs. 20A, D);

(1) expanded (Figs. 3A–E, G–I);

(2) very expanded (Fig. 3F).

The lunule non-expanded (state (0)) is very close to the base of the antennae. The lunule expanded is one time high the size of the scapus. The lunule very expanded (state (2)) is almost twice high the size of the scapus.

14. Antennae, distance between the scapes (L = 7; IC = 14; IR = 25):

(0) up to the width of one scape (Figs. 3A, B, D, F, H, I);

(1) at least twice the width of one scape (Figs. 3C, E, G).

15. Antennae, arista, pubescence (L = 13; IC = 23; IR = 62):

(0) bare;

(1) very short (almost inconspicuous) (Fig. 4I);

(2) short (shorter than the diameter of the base of the arista);

(3) long (longer than the diameter of the base of the arista) (Fig. 4J).

16. Antennal groove on the sides of the face, frontal view (L = 6; IC = 16; IR = 81):

(0) visible (Fig. 3E);

(1) not visible (Fig. 3G).

Cyrtomostoma gigas Hendel, 1909a has the most visible antennal groove among the genera. The antennal groove is sometimes difficult to visualize because the antennae may be covering this structure, which is located on the sides of the face below the scapes.

17. Face, lateral view, shape (L = 8; IC = 12; IR = 75):

(0) straight (Figs. 4E, F, H);

(1) concave (Fig. 4G).

18. Face, frontal view, height in relation to the frons (L = 4; IC = 25; IR = 76):

(0) shorter or as high as the frons (Figs. 3B–D, F, G, I);

(1) higher (Figs. 3A, E, H).

The height of the face was measured from the upper side of the scapes to the line between face and clypeus.

19. Clypeus, frontal view, height (L = 9; IC = 11; IR = 70):

(0) hidden, shorter than the diameter of the scape (Figs. 3A–E, G);

(1) protruding, higher or as high as the diameter of the scape (Figs. 3F, H, I).

20. Palpus, lateral view, shape (L = 1; IC = 100; IR = 100):

(0) not broad (reniform or triangular);

(2) broad (D-shaped or L-shaped).

The palpus of *Cyrtomostoma gigas* has a shape of a scalene triangle, but it is not as wide as the broad palpus present in the outgroups. The other genera of the ingroup present the palpus with a reniform shape.

Thorax (Figs. 5A–F, 6A–G)

21. Thorax, coloration (L = 2; IC = 100; IR = 100):

(0) yellow to dark brown (Figs. 5A–F);

(1) metallic, with blue or green reflections (Fig. 6D);

(2) shiny black.

The thorax metallic or shiny black is present only in the outgroups.

22. Scutum, microtrichia, pattern (L = 7; IC = 57; IR = 83):

(0) in bands (Figs. 5A, C, F);

(1) in spots (Fig. 5E);

(2) with no microtrichia at bases of setulae (Fig. 5D);

(3) uniformly distributed (Fig. 5B);

(4) in longitudinal stripes (Fig. 6D).

23. Supra-alar setae, number (L = 3; IC = 33; IR = 71):

(0) one;

(1) two.

Two supra-alar setae are only present in *Bothrometopa*, *Neomyennis*, *Pseudopterocalla* and some species of *Xanthacrona*.

24. Acrostichal setae (L = 3; IC = 33; IR = 60):

(0) present (Fig. 5C);

(1) absent (Fig. 5A).

The acrostichal setae are only absent in *Aciuroides*, *Cymatosus* and *Neoacanthoneura*.

25. Dorsocentral setae, number (L = 5; IC = 60; IR = 71):

(0) one (Figs. 5C, D);

(1) two (Figs. 5A, B, E);

(2) three;

(3) five.

Tetrapleura picta Shiner, 1868 and *Xanthacrona phyllochaeta* Hendel, 1909a are the only species with more than two dorsocentral setae.

26. Scutellum, apex, dorsal view, shape (L = 6; IC = 16; IR = 77):

(0) rounded, scutellum D-shaped (Figs. 5C–F);

(1) pointed, scutellum triangular shaped (Figs. 5A, B).

27. Scutellum, lateral view, shape (L = 5; IC = 20; IR = 33):

(0) flattened (Fig. 6D);

(1) convex (Figs. 6A, B).

28. Scutellum, apical setae, length in relation to the base of the scutellum (L = 8; IC = 12; IR = 69):

(0) up to the same width;

(1) longer (Fig. 5A).

29. Scutellum, modification in the shape (L = 1; IC = 100; IR = 100):

(0) swollen (Fig. 5F);

(1) not modified.

The scutellum slightly swollen or with additional and pronounced swellings is only present of *Xanthacrona*.

30. Anepisternum, setae, pattern (L = 12; IC = 8; IR = 50):

(0) one or two strong setae (Figs. 6A, C);

(1) row of more than two strong setae (Figs. 6B).

The species that present the state (1) of this character generally have the anepisternum with about 10 strong setae.

31. Anepisternum, setulae, density (L = 11; IC = 9; IR = 44):

(0) densely setulose;

(1) weakly setulose.

The anepisternum densely setulose have the space among the setulae smaller than the length of a setulae. The setulae on the anepisternum is better visualized in lateral view.

32. Katepisternum, setae, number (L = 2; IC = 50; IR = 50):

(0) one (Figs. 6A, B);

(1) two (Fig. 6C).

The katepisternum with two equally strong setae is only present in *Neomyennis*. Some specimens of *Xanthacrona* presents two setae on the katepisternum, but the second seta is not as strong as the first.

33. Anepimerum, setulae (L = 2; IC = 50; IR = 88):

(0) present (Fig. 6E);

(1) absent.

The absence of anepimeral setae or setulae is considered a symplesiomorphy of Ulidiidae that separates this family from the other Tephritoidea families (Kameneva & Korneyev 2010). However, the presence of anepimeral setulae (state 0 of this character) is here characterized by a small set of very weak setulae present in the upper region of the anepimerum, which differentiate from the setulose anepimerum present in other families. These weak setulae on the anepimerum can only be

visualized in lateral view.

34. Prosternum, setulae (L = 3; IC = 33; IR = 85):

(0) present (Fig. 6F);

(1) absent (Fig. 6G).

It was observed that the species with presence of setulae have the prosternum oval shaped, and the species that lack setulae have the prosternum rectangular shaped.

Wing (Figs. 7A–T)

35. Wing, pattern (L = 1; IC = 100; IR = 100):

(0) with dark spots (Figs. 7A–T);

(1) predominantly hyaline.

The species that present the state (1) of this character also have dark spots, but they occupy only a small portion of the wing. Solely the species of the outgroup present the state (1).

36. Vein Sc, apex, angle with the vein C (L = 3; IC = 66; IR = 66):

(0) smooth (curved) (Figs. 22A–F);

(1) about 45 degrees (Figs. 7A–D, F–T);

(2) about 90 degrees (Fig. 7E).

In the state (0), the vein Sc makes a slight curve before reaching the vein C, and in the state (1), the vein Sc continue straight until reaching the vein C.

37. Cell sc, height in relation to the height of cell c (L = 8; IC = 25; IR = 57):

(0) shorter (Figs. 7A, S);

(1) as high as the cell c (Figs. 7B, G–R, T);

(2) higher (Figs. 7C–F).

38. Vein R_1, dorsal side, setulae, pattern (L = 9; IC = 22; IR = 79):

(0) bare;

(1) setulose only in the apical half;

(2) entirely setulose.

39. Vein R_1, apex, distance to the apex of the vein Sc in relation to the length of the cell c (L = 10; IC = 20; IR = 52):

(0) close, less than the length of the cell c (Figs. 7D, E, H);

(1) as distant as the length of the cell c (Figs. 7A, B, G, I, J, L–R, T);

(2) distant, further than the length of the cell c (Figs. 7C, F, S).

40. Vein R_1, angle to the vein C (L = 1; IC = 100; IR = 100):

(0) gradually approaching the vein C (Figs. 7A–C, F, G, I–T);

(1) sharply curved to the vein C (Figs. 7D, E, H).

41. Cell c, upper expansion (L = 2; IC = 50; IR = 66):

(0) cell c is in a higher level than the cell sc (Figs. 7D, H);

(1) cell c is at the same level of the cell sc (Figs. 7A–C, E–G, I–T).

The state (0) of this character can be visualized by the sinuosity of the costal vein above the cell c.

42. Pterostigma, pigmentation (L = 10; IC = 10; IR = 62):

(0) with hyaline areas (Figs. 7A–D, H, I, K, L, P, S);

(1) completely pigmented (Figs. 7E–G, J, M–O, Q, R, T).

43. Pterostigma, sexual dimorphism (males with larger cell sc) (L = 8; IC = 12; IR = 46):

(0) present (Figs. 7C, F, G, J, K);

(1) absent (Figs. 7B, L, P).

44. Spurious vein between cell sc and vein R_{2+3} (L = 1; IC = 100; IR = 100):

(0) present (Fig. 7J);

(1) absent (Figs. 7A–I, K–T).

The additional crossvein between cell sc and vein R_{2+3} is only present in *Neomyennis*.

45. Cells r_1 and r_{2+3}, shape (L = 1; IC = 100; IR = 100):

(0) convex (Fig. 7M);

(1) flattened, on the same level of the other cells (Figs. 7A–L, N–T).

The state (0) character is only present in *Pseudopterocalla*. It is characterized by dilated cells, which differ from the usually flattened cells.

46. Vein R_{2+3}, sinuosity (L = 7; IC = 42; IR = 69):

(0) straight;

(1) almost straight (Fig. 22);

(2) slightly sinuous (Figs. 7A–C, F, G, I, J, L, N–T);

(3) strongly sinuous (Figs. 7D, E, H, K, M).

The sinuosity of the vein R_{2+3} is very variable among the Pterocallini and the establishment of states to describe the patterns of sinuosity was not possible. Therefore, this character describes superficially the sinuosity of the vein R_{2+3}.

47. Crossvein r-m, position in relation to cell dm (L = 8; IC = 25; IR = 53):

(0) basal (Figs. 7E, H, P);

(1) medial (Figs. 7A–D, F, G, I, K–O, R, S);

(2) apical (Figs. 7J, Q, T).

The state (2) was codified only in the species with the r-m very approximated to the crossvein dm-cu.

48. Crossvein r-m, length in relation to the length of the crossvein dm-cu (L = 15; IC = 13; IR = 40):

(0) one third (Figs. 7C, E, G, H, L, P);

(1) about half (Figs. 7A, B, D, F, I, K, M–O, R–T);

(2) almost the same size (Figs. 7J, Q).

49. Vein M, apex, position (L = 1; IC = 100; IR = 100):

(0) reaching the margin of the wing on the apex (Figs. 7A–G, I–T);

(1) reaching the margin of the wing posteriorly to the apex (Fig. 7H).

The state (1) of this character only occurs in *Megalaemyia*.

50. Vein M, before r-m, shape (L = 7; IC = 14; IR = 70):

(0) straight (Figs. 7A, B, E, G–L, O, P, S);

(1) curved (Figs. 7C, D, F, M, N, Q, R, T).

The vein M straight or curved before r-m can be distinghed by the angle that the cell d-m makes with the crossvein r-m.

Wendt (2012) used this character in the phylogenetic analysis of Richardiinae (Richardiidae).

51. Vein CuA_1, length (L = 9; IC = 11; IR = 69):

(0) reaching the posterior margin of the wing (Figs. 7C–F, H–J, P–R);

(1) not reaching the posterior margin of the wing (Figs. 7A, B, G, K–O, S, T).

52. Cell cup, posterior lobe (L = 8; IC = 12; IR = 50):

(0) present (Figs. 7C, G, J, N, R);

(1) absent (Figs. 7A, B, D–F, H–M, O–Q, S, T).

53. Cell cup, posterior lobe, length (L = 4; IC = 50; IR = 0):

(0) up to half the length of the cell cup (Figs. 7G, J, R);

(1) about the same length of the cell cup (Fig. 7N);

(2) two to three times the length of the cell cup (Fig. 7C);

(-) not applicable.

Although the retention index of this character resulted in 0, the character is described here for its possible use in other analysis.

54. Crossvein CuA_2, shape (L = 3; IC = 66; IR = 95):

(0) "S" shape (Figs. 7C, E, G, H, J, M, N, P–R, T);

(1) ">" or ")" shape (Figs. 7A, B, F, I, K, L, O, S);

(2) straight (Fig. 7D);

The state (0) of character was also applied to the species that present the posterior lobe of the cell cup elongated (character 53).

Legs (Figs. 8A–C)

55. Hind femur, preapical setae, pattern (L = 9; IC = 22; IR = 53):

(0) row of at least three strong setae (Fig. 8A);

(1) one pair of strong setae with more one or two strong setae on the side of the pair (Fig. 8B);

(2) one pair of strong setae (Fig. 8C).

56. Hind femur, ventral preapical setae (L = 3; IC = 33; IR = 71):

(0) present (Fig. 8B);

(1) absent (Figs. 8A, C).

Abdomen (Figs. 8D–H)

57. Abdomen, shape (L = 1; IC = 100; IR = 100):

(0) semiorbicular (Figs. 8D, F–H);

(1) semirectangular (Fig. 8E).

Aciuroides and *Lathrostigma* are the only genera with the abdomen semirectangular shaped.

58. Tergites, texture (L = 2; IC = 50; IR = 66):

(0) smooth (Figs. 8D, E, G, H);

(1) punctuated (Fig. 8F).

The tergites punctuated are only present in *Megalaemyia*.

59. Tergites, coloration (L = 5; IC = 80; IR = 90):

(0) brown with shiny grey and/or yellow microtrichia (Figs. 8G, H);

(1) grey to brown without shiny microtrichia (Fig. 8D);

(2) mostly yellow (Fig. 8E);

(3) shiny black (Fig. 8F);

(4) with metallic reflection.

60. Tergites, spots at bases of setulae (L = 1; IC = 100; IR = 100):

(0) present (Fig. 8H);

(1) absent (Figs. 8D–G).

The tergites with spots at bases of setulae are only present in two species of *Pterocalla*.

61. Sternites, ventral view, width (L = 2; IC = 50; IR = 85):

(0) narrow.

(1) wide.

The state (0) of this character is characterized by the sternites occupying about one third of the ventral area of the abdomen (only the center of the ventral side), while in the state (1), the sternites occupy at least half of the ventral area of the abdomen.

Female terminalia (Figs. 9A–J)

62. Oviscape, length in relation to the width (L = 14; IC = 21; IR = 54):

(0) as long as wide or slightly wider than long (Figs. 9B, F);

(1) 1.5 longer than wide (Figs. 9A, C, D);

(2) two times longer than wide;

(3) three times longer than wide (Fig. 9E).

In Lonchaeidae, Richardiidae, Ulidiidae and the rest of Higher Tephritoidea, oviscape is a name given to the tergosternum 7, which consists of the tergum and sternum 7 fused. In the ground plan of Tephritoidea, the tergum and sternum 7 are free from each other (Korneyev 1999).

63. Oviscape, mid-apical portion, ventral face, tegument extension (L = 10; IC = 10; IR = 40):

(0) present;

(1) absent.

This character is characterized by a small triangular lobe of the oviscape between the taeniae.

64. Taeniae, length in relation to the length of the oviscape (L = 11; IC = 18; IR = 60):

(0) shorter, up to half (Figs. 9C, D);

(1) about the same length (Fig. 9A);

(2) longer (Figs. 9B, E, F).

The taeniae of the eversible membrane consist of two sclerotized bands, and are stored inside the oviscape in the ground plan of Tephritoidea (Norrbom & Kim 1988;

Korneyev 1999).

65. Eversible membrane, length in relation to the length of the taeniae (L = 10; IC = 20; IR = 60):

(0) shorter, less than half (Figs. 9B, E, F);

(1) about the same length (Fig. 9A);

(2) longer, more than three times (Figs. 9C, D).

66. Eversible membrane, denticles, organization (L = 6; IC = 14; IR = 70):

(0) organized like scales (Fig. 9G);

(1) organized in transversal lines (Fig. 9H);

(-) not applicable.

The eversible membrane bare or heavily toothed are derived states of Tephritoidea found in Ulidiidae, Platystomatidae and Tephritidae (Korneyev 1999). *Pterotaenia fasciata* (Wiedemann, 1830) is the only species analyzed that lacks denticles on the eversible membrane.

67. Eversible membrane, denticles, margin (L = 4; IC = 50; IR = 84):

(0) rounded (Fig. 9G);

(1) serrated (Fig. 9H);

(2) pointed;

(-) not applicable.

68. Segment 8, width in relation to the diameter of the hind tarsus (L = 2; IC = 100; IR = 100):

(0) narrower;

(1) about the same diameter;

(2) at least two times.

The segment 8, which consists of a pair of longitudinal sclerotized structures, when is fused with the apical part of the terminalia, is called aculeus. In Ulidiidae, these two structures are not fused, so it is called simply segment 8 (Norrbom & Kim 1988). The hind tarsus was chosen as a parameter of comparison to the width of the segment 8

because its width does not vary among the species.

69. Segment 8, transversal marks on the dorsal and ventral side (L = 3; IC = 33; IR = 80):

(0) present (Fig. 9J);

(1) absent (Fig. I).

70. Cerci, lateral view, shape (L = 1; IC = 100; IR = 100):

(0) globose;

(1) flattened.

Kameneva (2012) commented that the flattened cerci (state (1)) is one of the shared characters of the group that includes *Aciuroides*, *Apterocerina*, *Coscinum* (not included in the analysis), *Cyrtomostoma*, *Elapata* (not included in the analysis), *Lathrostigma*, *Micropterocerus* (not included in the analysis), *Pterocerina* and *Tetrapleura*.

71. Cerci, apex, dorsal view, shape (L = 4; IC = 50; IR = 84):

(0) oval (Fig. 9J);

(1) pointed (Fig. 9I);

(2) truncated.

In Tephritoidea, the cerci are the acute or oval apical portion, which bears six to eigth setae (Korneyev 1999). The state (2) of this character is characterized by the margin of the cerci apex almost squared.

72. Spermathecae, number (L = 1; IC = 100; IR = 100):

(0) two;

(1) three.

Three spermathecae are present in the ground plan of Tephritoidea, with two of them sharing the same duct (Korneyev 1999). The presence of three spermathecae is one of the characters shared by the species of Pterocallini (Kameneva & Korneyev 2006).

Male terminalia (Figs. 10A–G)

The male terminalia of *Plagiocephalus intermedius* was assumed to be equal to the

terminalia of the other species of the genus.

73. Epandrium, posterior view, shape (L = 5; IC = 20; IR = 55):

(0) elongate oval (Figs. 10C, 23A, B);

(1) short oval (almost rounded) (Figs. 10A, B, D–G).

In the ground plan of Tephritoidea, the epandrium has a shape of inverted-U, which is derived from the tergite 9 (Korneyev 1999; White et al. 1999).

74. Lateral surstylus, lateral view, connection with the epandrium (L = 7; IC = 28; IR = 61):

(0) strongly connected;

(1) weakly connected;

(2) distinctly weakly connected.

In the ground plan of Tephritoidea and in many ulidiids, the lateral surstylus is not fused to the epandrium (Korneyev 1999; White et al. 1999). In the state (1) of this character, the membrane between the lateral surstylus and the epandrium is poorly visible, and in the state (2), the membrane is easily viewed.

75. Lateral surstylus, lateral view, size in relation to the epandrium (L = 4; IC = 25; IR = 62):

(0) about half the length of the epandrium;

(1) same length or longer.

76. Lateral surstylus, lateral view, shape (L = 4; IC = 75; IR = 87):

(0) curved and concave;

(1) curved and flattened;

(2) curved and pointed;

(3) straight and flattened.

The shape of the lateral surstylus is very variable among the Pterocallini, so it would be necessary to create many states to describe each different form of the lateral surstylus. Therefore, this character describes superficially this structure.

77. Lateral surstylus, apex, posterior view, distance between each other (L = 3; IC = 33; IR = 66):

(0) close, almost touching (Figs. 10D, E, G);

(1) far away, not touching (Figs. 10A–C, F).

78. Medial surstylus, anterior view, connection with the lateral surstylus (L = 5; IC = 40; IR = 50):

(0) connected in the apex;

(1) almost completely fused to the lateral surstylus;

(2) connected in the base.

The homology of the medial surstylus of Tephritoidea is not clear, but probably it is derived from the single surstylus of the other acalyptrates (White et al. 1999).

79. Medial surstylus, anterior view, shape (L = 2; IC = 50; IR = 92):

(0) v-shaped (Figs. 23A, B);

(1) c-shaped.

80. Presinsetae (L = 2; IC = 50; IR = 50):

(0) present (Figs. 10A–G);

(1) absent.

In the ground plan of Tephritoidea, the medial surstylus bears two or three thickened setae, called presinsetae (Korneyev 1999). The presisetae are absent only in Lipsanini (outgroup) and in *Xanthacrona phyllochaeta*.

81. Presinsetae, shape (L = 3; IC = 66; IR = 83):

(0) claw-like (Figs. 23A, B);

(1) blunt-like;

(2) spine-like;

(-) not applicable.

82. Presinsetae, inner surface (L = 2; IC = 50; IR = 80):

(0) serrated (Figs. 23A, B);

(1) smooth;

(-) not applicable.

The presinsetae with inner serrated surface in only present in *Paragorgopis* and *Plagiocephalus*.

83. Presinsetae, number and position (L = 4; IC = 100; IR = 100):

(0) one basal (Fig. 10D);

(1) one medial (Figs. 10F, G);

(2) one preapical (Fig. 10B);

(3) two preapical (Figs. 10A, C, 23A, B);

(4) four distributed (Fig. 10E);

(-) not applicable.

In this case, I opted to construct a compound character for trying not to lose the homology of the presinsetae, since position and number of presinsetae are related conditions.

84. Presinsetae, preapical pair, distance between each other (L = 2; IC = 50; IR = 85):

(0) close, less than the diameter of one presinseta (Figs. 10A, 23A, B);

(1) distant, more than the diameter of one presinseta (Fig. 10C);

(-) not applicable.

85. Presinsetae, preapical pair, posterior view, position in relation to each another (L = 3; IC = 33; IR = 60):

(0) second presinseta above the first (Figs. 10A, 23A, B);

(1) on the same level (Fig. 10C);

(-) not applicable.

86. Phallapodeme, opening connected to the basiphallus (L = 8; IC = 25; IR = 50):

(0) large opening, almost V-shaped;

(1) medium opening, Y-shaped (Figs. 23C, D);

(2) small opening, almost I-shaped.

Phallapodeme is a sclerite that articulates with the base of the phallus and have lateral arms that are fused to the hypandrium (Fig. 2D) (White et al. 1999).

87. Basiphallus, shape (L = 4; IC = 25; IR = 50):

(0) D-shaped (Figs. 23C, D);

(1) O-shaped.

In the ground plan of Tephritoidea, the phallus is formed by a sclerotized tube or ring, called basiphallus, and a long and flexible distiphallus (Korneyev 1999).

88. Distiphallus, length in relation to the length of the abdomen (L = 10; IC = 20; IR = 42):

(0) short, up to one third;

(1) long, almost the same length;

(2) extremely long, longer than the abdomen.

In Ulidiidae and Richardiidae, the phallus is tightly coiled and stored in the right side of the abdomen (Korneyev 1999). The state (2) of this character only occurs in the outgroups and in *Xanthacrona phyllochaeta*.

89. Distiphallus, bands (L = 11; IC = 45; IR = 57):

(0) bare (Fig. 10F);

(1) short microtrichose (Fig. 10G);

(2) scaly;

(3) microspinulose;

(4) setulose;

(5) setulose and spinulose (Fig. 10E).

The distiphallus bare or microtrichose is one of the characteristics that describe Pterocallini (Kameneva & Korneyev 2006). Besides microtrichia, other very small structures, like scales or spines, were here observed in some species of Pterocallini. In Tephritoidea, the distiphallus can be bare, bearing microtrichia, setae, scales or spines (Korneyev 1999; White et al. 1999).

90. Proctiger, posterior view, shape (L = 7; IC = 57; IR = 83):

(0) globose (Fig. 10A);

(1) squared (Figs. 23A, B);

(2) divided in the 2/3 basal (Fig. 10E);

(3) completely divided (Fig. 10G);

(4) forming two lobe-like structures.

91. Ejaculatory apodeme, length in relation to the epandrium (L = 7; IC = 14; IR = 33):

(0) up to the same length;

(1) longer.

Phylogeny of Pterocallini

The parsimony analysis under equal weighting resulted in 27 most parsimonious trees. The strict consensus of the trees (Fig. 11) has 565 steps, IC of 25 and IR of 61. The analysis under implied weighting with $k = 1–13$ resulted in one most parsimonious tree, whereas the analysis using $k = 14–30$ generated six most parsimonious tree. The number of steps, IC, IR, *fit* and number of trees of the analysis using different k are presented in Table 2.

The parsimony analysis under implied weighting resulted in a total of five distinct trees. An analysis set to $k = 1$ (Fig. 12) resulted in one topology, a second optimal tree was generated when $2 \leq k \leq 5$ (Fig. 13), a third topology resulted when $6 \leq k \leq 9$ (Fig. 14), a fourth optimal tree resulted when $10 \leq k \leq 13$ (Fig. 15), and a fifth optimal tree through a strict consensus was generated when $14 \leq k \leq 30$ (Fig. 16). The topology gained stability from k values above 14. The tree selected to serve as the main hypothesis of relationships of Pterocallini was the phylogeny resulted from the analysis under $10 \leq k \leq 13$ (Fig. 15). The reasons for the choice of the preferred tree are presented in the Discussion section. The characters were optimized (Fig. 17) and the Relative Bremer Support was plotted only onto the preferred tree (Fig. 18).

Taxonomy of *Plagiocephalus* Wiedemann

Plagiocephalus Wiedemann, 1830
(Figs. 19–23)

Wiedemann, 1830b: 12, 15; Westwood, 1849: 235; Osten-Sacken, 1881: 478; Hendel, 1911: 4, 52; Cresson, 1923: 258; Frey, 1926: 47; Carrera, 1950: 261; Aczél, 1951: 421; Steyskal, 1963: 511; 1964: 400; 1968: 54.21; Kameneva, 2004b: 15.

Plagiocephalus Wiedemann, 1830b: 15. Type species: *Achias lobularis* (Wiedemann, 1830a): 555 (by monotypy).

Stylophthalmyia Frey, 1926: 45 (synonymized by Steyskal, 1963: 511). Type species: *Stylophthalmyia fascipennis* Frey, 1926: 46 (by original designation).

Ophryoterpnomyia Hendel, 1936: 76 (synonymized by Carrera, 1950: 260). Type species: *Terpnomyia latifrons* Hendel, 1909a: 18 (by original designation).

Paragoniaeola Blanchard, 1938a: 370 (synonymized by Aczél, 1951: 399). Type species: *Paragoniaeola tanycephala* Blanchard, 1938a: 371 (by original designation).

Eupterocerina Blanchard, 1938b: 91 (synonymized by Steyskal, 1968: 54.21). Type species: *Eupterocerina conjucta* Blanchard, 1938b: 91 (by original designation).

Willineria Blanchard, 1951: 32 (synonymized by Steyskal, 1964: 490). Type species: *Willineria orfilai* Blanchard, 1951: 32 (by original designation).

Diagnosis. Male with stalked eyes, frons wider than long (moderately wide in female). Thorax and abdomen brownish with pattern of yellowish-grey microtrichia; one supra-alar and two dorsocentral setae. Sexual dimorphism in pterostigma absent in males; vein R_1 setulose on apical half; vein R_{2+3} almost straight; vein r-m at apical 2/5 of d-m cell; cell cup with short posterior lobe; wing hyaline with four main dark-brown bands: discal band, radial-medial band, subapical band and anterior apical band. Abdominal tergites 3–5 subequal in both sexes. Female with tergite 6 short, hidden under tergite 5, with several short marginal setulae; sternites 4–6 without apodemes. Male terminalia with distiphallus microtrichose at the apical 2/3, very elongated; ejaculatory apodeme with apical portion at least as long as its fan-like portion; epandrium elongate oval and setulose; medial surstylus bearing two subequal prensisetae with small denticles on inner surface. Female with three brown and smooth spermathecae; oviscape brown, setulose, longer than the four preceding tergites together; segment 8 long; cerci oval, slightly turned upwards, dorsally with one basal, one subapical and two apical pairs of setae.

Description. Head: Male (Figs. 20A, D): Wider than the thorax; in frontal view wider than higher (at least five times the width of eye); eyes stalked; entirely microtrichose; compound eye higher than the gena; inner vertical setae parallel; outer vertical, postocellar and ocellar setae divergent; upper orbital and inferior orbital setae reclinate; ocellar triangle brown to black; dorsolateral and anterior portions of occiput brown; frons gold, with darker spots, wider than long and with sparsely distributed black setulae; gena with black setulae and developed vibrissa; antennal grooves absent; scape, pedicel and first flagellomere yellow to gold; first flagellomere oval, about 2.5 times the length of pedicel; arista brown with very short pubescence, about 3.5 times the length of first flagellomere; clypeus with white microtrichia; palpus not extending beyond anterior oral margin, with black setulae on apex; proboscis capitate covered with setulae. Female (Figs. 21A, D, G): Similar to male, except: in frontal view wider than higher (less than four times the width of eye); eyes not stalked; frons with two brown to black spots anterior to ocellar triangle; face convex with black spot between antennae and two transversal brown spots above clypeus; gena with C-shaped spot of brown microtrichia.

Thorax (Figs. 20B, E, 21B, E, H): Brownish black with patterns of yellow-grey microtrichia; scutum with brown microtricose pattern; postpronotal lobe, scutellum, subscutellum and mediotergite mostly shiny brown; scutellum with a yellow-grey microtrichose stripe reaching the subscutellum; one postsutural supra-alar seta, one postalar seta, one intra-alar seta, two dorsocentral setae and two scutellar setae; anepisternum setulose and with up to 10 setae; katepisternum with one seta.

Wing (Fig. 22): Humeral break distinct; vein C between veins Sc and R_1 almost straight; cell c with brown spots; pterostigma unmodified, five to seven times as long as wide; vein R_1 setulose on apical half; vein R_{2+3} bare and almost straight; vein R_{4+5} bare, ending in the middle of apex; vein r-m at apical 2/5 of cell d-m; cell cup with very short posterior lobe; vein A_1+CuA_2 reaching the posterior margin; wing hyaline with pattern of four main bands; discal band from middle of cell sc inclined to posterior margin close to vein CuA_1; radial-medial band starts from apex of cell sc and reaches the vein r-m; subapical band from vein CuA_1 crossing the wing to the 5/6 of vein C; anterior apical band from final portion of vein C bypassing the apex. Upper calypter slightly longer than lower calypter, white and with white fringe. Halter white to yellow.

Legs (Figs. 20C, F, 21C, F, I): Unmodified, moderately setulose and with coloration brown or yellow.

Abdomen: Dark brown, with areas of yellow-grey and brown microtrichia at anterior and posterior margins of tergites; uniformly setulose; male with tergite 5 without microtrichia; female with tergite 5 shorter than the 4, and tergite 6 smaller, hidden under the 5, without microtrichia and with 4–5 short marginal setulae; sternites 4–6 without apodemes.

Terminalia: Male (Figs. 2A–D, 23): Ejaculatory apodeme with the apical portion at least as long as its fan-like portion; epandrium elongate oval and setulose; medial surstylus "V" shaped, with each apex connected to lateral surstylus; two subequal prensisetae with small denticles on the inner surface positioned subapically on medial surstylus; lateral surstylus with anterior lobe longer than the posterior lobe; basiphallus D-shaped connected with phallapodeme; phallapodeme Y-shaped with apex slightly surpassing the hypandrium; phallapodemic arms connected with hypandrium with few small setulae; phallus with setulae at the apical 2/3, elongated and with no glans on apex. Female (Figs. 2E, F): Three brown and smooth spermathecae; oviscape brown, setulose, longer than the four preceding tergites together; segment 8 long; cerci oval, slightly turned upwards, and dorsally with one basal, one subapical and two apical pairs of setae.

Distribution. Neotropical (Mexico, Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Venezuela, Trinidad, Colombia, Ecuador, Peru, Bolivia, Brazil, Paraguay and Argentina) (Fig. 24).

Plagiocephalus lobularis (Wiedemann, 1830)
(Figs. 19A, B, 20A–C, 21A–C, 22A–B, 23A, C)

Wiedemann, 1830b: 15; Macquart, 1843: 213 (*Plagiocephala lobularis*); Hendel, 1909b: 47; Westwood, 1849: 235; Frey, 1926: 47; Carrera, 1950: 262, 265 (*Plagiocephalus latifrons* (misidentification; see Steyskal, 1963); Aczél, 1951: 422; Hennig, 1952: 616; Steyskal, 1963: 512, 1968: 54.21; Kameneva, 2004b: 16.

Achias lobularis: Wiedemann, 1830a: 555; Macquart, 1835: 260. (Lectotype male, ZMUC) (examined by photographs).

Paragoniaeola tanycephala Blanchard, 1938a: 371 (synonymized by Aczél, 1951) (Holotype male, INTA) (examined by photographs).

Eupterocerina conjuncta Blanchard, 1938b: 91 (synonymized by Steyskal, 1968) (Holotype female).

Ophryoterpnomyia zikani Capoor, 1954: 205 (synonymized by Steyskal, 1963) (Holotype female, Instituto Oswaldo Cruz (CEIOC) (n° 5787, 4541–4543)).

Type material. Lectotype of *Achias lobularis* (designed by Kameneva, 2004b) (male): "P. lobularis / Wied. / Brazils / Lund", "Mus. / Westerm.", "Syntype male / Achias lobularis / Wiedemann / 1830 / des. V. Korneyev / XII.2003", "Syntypus", "ZMUC 00025500" (Figs. 19A, B).

Diagnosis. *Plagiocephalus lobularis* can be differentiated from *P. latifrons* and *P. intermedius* by the shortest eyestalks (1.42–3.94 mm) (Fig. 20A); female parafacialia yellow (Fig. 21A); radial-medial band well connected with discal band (Figs. 22A, B), and male wing with three posterior lobes (Fig. 22A). The species can also be distinguished by male frons with dark gold spot on anterior portion of ocellar triangle (Fig. 20B); male with purplish black spot from ventral side of the head up to face and part of the parafacialia (Fig. 20A); scape dark gold to brown (Figs. 20A, 21A); pedicel and first flagellomere gold, sometimes with darker marks (Figs. 20A, 21A); male palpus brown (Fig. 20A) and female palpus yellow (Fig. 21A); proboscis brown with brown and yellow setulae. Wing with vein r-m located before vein R_1 apex (Figs. 22A, B); cell cup yellow and in males closed by an almost straight vein (Fig. 22A); cells c and sc and base of discal band with darker coloration than the other bands (Figs. 22A, B); male discal and subapical bands forming a rounded angle (Fig. 22A). Brown legs with tarsi lighter and fore coxa yellow; male fore femur with base yellow (Fig. 20C); female fore femur yellow with a brown ring subbasal on femur (Fig. 21C).

Measurements: Male: body (2.37–3.52 mm); wing (4.35–5.34 mm). Female: body (2.49–3.75 mm); wing (4.35–5.82 mm); oviscape (1.0–1.5 mm).

Examined material. ARGENTINA: Misiónes, Iguazú (25.6036 S, 54.5558 W), 04–10.x.1927, R. C & E. M. Shannon *leg.*, 1 male (Det.: E. Kameneva, 2001) (USNM).

BRAZIL: Ceará: Ibiapaba, Cachoeira Samambaia, 21.x.2011, Gomes & Duarte *leg*., 1 female (DZUP); Ubajara, Parque Nacional do Ubajara, Cachoeira do Cafundó (3.8369 S, 40.9097 W), 01–15.i.2013, F. Limeira-de-Oliveira & J. S. Pinto Júnior *leg*., 1 male (CZMA). Goiás: (Est. Goyaz), Campinas, i–1936, R. Spitz *leg*., 1 female (MNRJ) and 5 females (MZSP); Goianesia, ix.1969, H. Ebert *leg*., 2 females (MZSP). Mato Grosso: Maracaju, ii.1937, 1 female (USNM). Mato Grosso do Sul: Aquidauana (20.4344 S, 55.6558 W), 15–26.x.2011, Lamas, Nihei & eq. *leg*., 1 female (MZSP). Paraná: Antonina, Reserva Rio Cachoeira (25.3119 S, 48.6717 W), 50 m, 23–27.i.2017, A. C. Domahovski *leg*., 1 male and 1 female (DZUP); Curitiba, Jardim Botânico (25.4421 S, 49.2388 W), 05.iv.2015, O. Aguirre-Obando *leg*., 1 male (DZUP); idem, Universidade Federal do Paraná, Centro Politécnico, Mata Viva (25.4458 S, 49.2324 W), 921 m, 28.vii–11.viii.2015, L. Wendt *leg*., 1 male (DZUP); ibidem, 11–25.viii.2015, 2 females (DZUP); ibidem, 09–24.ix.2015, 1 female (DZUP); ibidem, 09–23.x.2015, 1 male (DZUP); ibidem, 18.xi–03.xii.2015, 1 female (DZUP); ibidem, 08–25.i.2016, 1 male and 2 females (DZUP); ibidem, 11–25.ii.2016, 1 male and 2 females (DZUP); ibidem, 26.ii–14.iii.2016, 2 males and 1 female (DZUP); ibidem, 14–28.iii.2016, 3 males and 2 females (DZUP); ibidem, 28.iii–13.iv.2016, 2 males and 2 females (DZUP); ibidem, 13–28.iv.2016, 2 males and 4 females (DZUP); ibidem, 25.viii–09.ix.2016, 1 female (DZUP); idem, 6–9.xii.2016, A. C. Vasconcelos *leg*., 1 female (DZUP); ibidem, 21–23.ii.2017, 1 male and 1 female (DZUP); ibidem, 28.iii–03.iv.2017, 1 male (DZUP); idem, 15.ix.2017, S. Silva *leg*., 3 females (DZUP); Paranaguá, Floresta Estadual do Palmito (25.5688 S, 48.5355 W), 16–17.vii.2014, Leviski, Siewert & Queiroz-Santos *leg*., 2 males (DZUP); São José dos Pinhais (25.6047 S, 49.1933 W), 897 m, xi.2016, A. C. Domahovski *leg*., 2 females (DZUP); ibidem, xii.2016, 1 female (DZUP). Pernambuco: Bonito, Cachoeira Véu da Noiva (8.5423 S, 35.715 W), 510 m, 25.iii.2015, F. Bravo *leg*., 1 male (DZUP). Rio de Janeiro: Angra, Japuíba "Japuhyba" (22.9949 S, 44.2920 W), i.1985, E. Dorio & T. Travasso *leg*., 1 female (MNRJ); Casimiro de Abreu, Reserva Biológica da União, Trilha Buracão (22.4240 S, 42.0391 W), 14.i–14.ii.2014, Eq. Col. Biota Diptera Fluminense *leg*., 1 female (MNRJ); Rio de Janeiro, x–xii.1937–1.1938, R. C. Shannon *leg*., 2 females (USNM); idem, ix.1938, 1 female (USNM); idem, x.1938, YelFevServ. MESBrazil, 9 females (Det.: G. Steyskal, 1962) (USNM); ibidem,

i.1939, 1 female (USNM); idem, 08.xi.1933, H. Lopes Souza *leg*., "*Terpnomyia latifrons*", 1 female (MNRJ); idem, ix.1938, Serv. Febre Amarela MESBrazil, 1 female (USNM); idem, "Dist. Federal", x.1937, Serv. Febre Amarela MESBrazil, 1 male (USNM); idem, xii.1938, Serv. Febre Amarela MESBrazil, 1 female (USNM); ibidem, xiii.1938, 1 female (USNM); idem, ix.1938, R. C. Shannon *leg.*, YelFevServ. MESBrazil, 1 female (USNM); Jacarepaguá, Repr. Rio Grande, iii.1968, M. Alvarenga *leg*., 1 female (MZSP); Nova Friburgo, Caledônia, 2219 m, ii.2001, E. & P. Grossi *leg*., 1 male (DZUP). idem, Sans Souci (22.2808 S, 42.5121 W), 06.i.2010, 2 males (DZUP). idem, Sítio Caturama, 1050 m, 30.xii.2008, P. Grossi *leg.*, 1 male (DZUP); Petrópolis, Taquara (22.6185 S, 43.2301 W), 28.xii.197?, H. S. Lopes *leg.*, 1 male (MZSP); ibidem, 13.xii.1970, 1 female (MZSP); ibidem, 28.xii.1970, 1 female (MZSP); ibidem, 01.i.1971, 1 female (MZSP); ibidem, 03.i.1971, 3 females (MZSP); ibidem, ?.i.1971, 1 female (MZSP); ibidem, 11.i.1971, 1 female (MZSP); ibidem, 14.i.1971, 1 male and 3 females (MZSP); ibidem, 06.ii.1971, 1 male and 2 females (MZSP); ibidem, 07.ii.1971, 1 male and 2 females (MZSP); ibidem, 14.ii.1972, 2 females (MZSP); ibidem, 15.ii.1972, 3 females (MZSP); ibidem, 11.vi.1972, 1 female (MZSP) and 7 females (MZSP). Santa Catarina: Florianópolis, vii.1960, Casemiro *leg*., 1 female (MZSP); Joinville, 27.i.1972, H. S. Lopes *leg*., 1 female (MZSP); Nova Teutônia (27.1833 S, 52.3833 W), 24.x.1936, Fritz Plaumann *leg*., Brit. Mus. 1936–256, A. E. Whittington (2004), 1 male (NHMUK 010862540); ibidem, 29.xi.1937, Brit. Mus. 1938–40, 2 females (NHMUK 010862538, NHMUK 010862539); ibidem, 28.iii.1938, Brit. Mus. 1938–312, 1 female (NHMUK 010862537); ibidem, ii.1967, 1 female (MZSP); ibidem, ii.1969, 1 female (MZSP); ibidem, x.1969, 2 females (MZSP); ibidem, xi.1970, 1 female (MZSP); ibidem, vii.1971, 1 female (MZSP). São Paulo: Andes, 1955, M. Carrera *leg*., 1 male and 2 females (MZSP); Barueri, ?.ii.1966, K. Lenko *leg*., 1 female (MZSP); Butantan, 02.vii.1979, H. S. Lopes *leg*., 1 female (MZSP); ibidem, 12.vii.1979, 1 female (MZSP); idem, Horta O. Cruz, 06.viii.1969, L.T.F. *leg*., 1 male (MZSP); ibidem, 08.viii.1979, 1 male (MZSP); ibidem, 11.viii.1971, 2 males and 3 females (MZSP); Cantareira, Chapadão (23.4142 S, 46.6000 W), viii.1946, Barreto *leg*., 1 female (MZSP); Rio Paraná, Porto Cabral, 01–25.iv.1944, Trav. Fo., Carrera & E. Dente *leg*., 1 male (MZSP); São José dos Campos,

15–22.viii.1997, Eurico R. de Paulo *leg*., 1 female (LACM); ibidem, 07–14.ix.1997, 1 female (LACM).

Distribution. Brazil (Goiás, Mato Grosso do Sul, São Paulo, Rio de Janeiro and Santa Catarina), Paraguay and Argentina. New records: Brazil (Ceará, Pernambuco and Paraná) (Fig. 25).

Comments. Blanchard (1938a, 1938b) deposited the holotypes of the descriptions in his personal collection, thus only the material of *Paragoniaeola tanycephala* could be tracked (INTA).

Plagiocephalus latifrons (Hendel, 1909)
(Figs. 19C, D, 20D–F, 21D–F, 22C–D, 23B, D)

Aczél, 1951: 421; Steyskal, 1963: 512; 1964: 400; 1968: 54.21; Kameneva, 2004b: 18; Kameneva et al., 2017: 127.

Terpnomyia latifrons: Hendel, 1909a: 18; 1909b: 31; pl. 2, figs. 30, 31 (Syntypes: 3 females, MTD; 1 female, NHMW) (examined by photographs).

Ophryoterpnomyia latifrons: Hendel, 1936: 76 (synonymized by Carrera, 1950) (Syntypes: 9 females, NHMW).

Stylophthalmyia fascipennis Frey, 1926: 46 (synonymized by Steyskal, 1963) (Holotype male, MZH) (examined by photographs).

Willineria orfilai Blanchard, 1951: 32 (synonymized by Steyskal, 1964) (Holotype male, Museo de Ciencias Naturales de Salta (INESalt)).

Type material. Syntypes of *Terpnomyia latifrons* (4 females): “Bolivia - Mapiri / 21.I.03 / S. Carlos 800 m”, “Terpnomyia latifrons / det. F. Hendel”, “Cotypus”; “Bolivia - Mapiri / 5.III.03 / Sarampioni 700 m”, “Terpnomyia latifrons / det. F. Hendel”, “Cotypus”, “Peru - Urubambafl. / 10.IX.03 / Umahuankilia”; “Terpnomyia latifrons / det. F. Hendel”, “Cotypus”, “Staatl. Museum für/ Tierkunde Dresden/ Coll. W. Schnuse, 1911” (MTD) (Figs. 19C, D); “Peru - Urubambafl./ 13.IX.03 / Umahuankilia”, “Terpnomyia latifrons / det. F. Hendel”, “Paratype”, “Coll. Hendel” (NHMW).

Diagnosis. *Plagiocephalus latifrons* can be differentiated from *P. lobularis* and *P. intermedius* by the longest eyestalks (5.08–18.08 mm) (Fig. 20D); female parafacialia black (Fig. 21D); radial-medial band with base almost as narrow as the apex, at most barely touching the discal band (Figs. 22C, D). The species can also be distinguished by male frons with gold spot on anterior portion of ocellar triangle (Fig. 20E); male face yellowish white, with region close to antennae yellower (Fig. 20D); male scape, pedicel and first flagellomere entirely yellow (Fig. 20D), and female scape, pedicel and first flagellomere gold with apex sometimes darker (Fig. 21D); palpus yellow (Fig. 21D); male proboscis yellow with yellow setulae, and female proboscis reddish yellow with brown and yellow setulae. Male wing of normal outline, without posterior lobes (Fig. 22C); vein r-m at the level of vein R_1 apex (Figs. 22C, D). Male fore and mid leg entirely yellow, and hind leg yellow to gold (Fig. 20F); female legs brown with tarsi lighter, and fore femur yellowish on the apex (Fig. 20F).
Measurements: Male: body (2.55–3.75 mm); wing (4.05–6.8 mm). Female: body (2.85–4.00 mm); wing (4.75–6.48 mm); oviscape (1.05–1.5 mm).

Examined material. BELIZE: Stann Creek Valley, 06.iv.1979, B. Bowers *leg*., 4 males (USNM). BRAZIL: Acre: Cruzeiro do Sul, Rio Moa (7.6172 S, 72.7708 W), 19–28.xi.1996, J. A. Rafael, J. Vidal & R. L. Menezes *leg*., 1 female wing (INPA). Amapá: Serra do Navio, 13.x.1957, J. Lane *leg*., 1 female (MZSP). Amazonas: Barcelos, Rio Demeni Pirico (0.325 S, 62.7892 W), viii.2008, A. Silva & R. Machado *leg*., 1 female (INPA); Ipixuna, Rio Gregório, Com. Lago Grande (7.1699 S, 70.8195 W), 18–23.v.2011, J. A. Rafael, J. T. Câmara, R. F. Silva, A. Somavilla, C. Gonçalves *leg*., 1 female (INPA); idem, Rio Liberdade, Estirão da Preta (7.363 S, 71.8686 W), 11–15.v.2011, J. A. Rafael, J. T. Câmara, R. F. Silva, A. Somavilla, C. Gonçalves & A. Agudelo *leg*., 1 female (INPA); ibidem, J. A. Rafael, J. T. Câmara, R. F. Silva, A. Somavilla & C. Gonçalves *leg*., 2 females (INPA); Manaus, Campus Universitário, 23.vi.1979, J. A. Rafael *leg*., 1 female (INPA); idem, Reserva Ducke (2.9166 S, 59.9833 W), 20 m, 07–21.xii.1994, J. A. Rafael & J. Vidal *leg*., 1 female (INPA); idem, 09.viii.2000, J. Vidal & A. F. Oliveira *leg*., 1 male (INPA); ibidem, 12.ix.2000, 1 male (INPA); ibidem, 26.x.2000, 2 males (INPA); ibidem, 27.x.2000, 1 female (INPA);

ibidem, 28.xi.2000, 1 male (INPA); ibidem, 24.v.2001, 1 male (INPA); idem, ix.2001, J. Vidal *leg*., 1 female (INPA); idem, ZF2 km-14 Torre (2.5892 S, 60.1153 W), 19–22.iii.2004, J. A. Rafael, C. S. Motta, F. F. Xavier F, A. Silva F & J. T. Câmara *leg*., 1 female (INPA); idem, 18–21.v.2004, J. A. Rafael, F. B. Baccaro, F. F. Xavier & A. Silva *leg*., 1 female (INPA); idem, 12–15.x.2004, J. A. Rafael, C. S. Motta, F. F. Xavier, A. Silva F & S. Trovisco *leg*., 1 female (INPA); idem, 17–21.viii.2017, J. A. Rafael, A. C. Vasconcelos, F. F. Xavier, T. Mahlmann, S. Lima & B. Oliveira *leg*., 1 male (INPA); Novo Aripuanã, Reserva Soka (5.2647 S, 60.1188 W), 28.iv–06.v.1999, R. L. Ferreira, R. A Rocha, J. Vidal & R. S. Leite *leg.*, 2 females (INPA); idem, 17–25.viii.1999, J. Vidal & A. L. Henriques *leg.*, 1 male and 4 females (INPA); Pq. N. Jau, Ig. Miracutu, Ig. do Gerlei (1.9500 S, 61.8167 W), 23–28.vii.1995, J. A. Rafael & J. Vidal *leg*., 1 female (INPA); Rio Javari, Retirão do Equador, x.1979, Alvarenga *leg*., 2 females (MZSP); São Gabriel da Cachoeira, Morro dos Seis Lagos, 800 m, 28.ix–6.x.1990, J. Vidal & J. A. Rafael *leg.*, 1 male (INPA). Maranhão: Bom Jardim, REBIO-Res. Biol. Gorupi, 02–11.ix.2010, D. W. A. Marques, E. A. S. Barbosa, J. A. Silva & M. M. Abreu *leg*., 1 female (CZMA). Pará: Belém, APEG Forest, x.1969, T. H. G. Aitken *leg.*, 1 female (USNM); Óbidos, Colônia São Tomé (1.8461 S, 55.0397 W), 01–11.ix.2001, J. A. Rafael & J. Vidal *leg*., 1 female (INPA); idem, Faz. Parujá (1.6225 S, 55.3872 W), 05–11.ix.2000, J. A. Rafael & J. F. Vidal *leg.*, 1 male (INPA); idem, Sítio Curuó (1.7842 S, 55.1181 W), 29.viii–08.ix.2001, J. A. Rafael & J. Vidal *leg*., 1 female (INPA). Rondônia: 62 Km SE Ariquemes (10.2418 S, 62.5492 W), 17–24.iii.1989, W. J. Hanson *leg*., 4 females (LACM); idem, 15–22.iii.1991, W. Hanson & G. Bohart *leg*., 1 female (LACM); idem, 13–25.iv.1992, W. J. Hanson *leg*., 1 female (LACM); ibidem, 8–20.xi.1994, 5 females (LACM); ibidem, 7–18.xi.1995, 1 female (LACM); ibidem, 22–31.x.1997, 1 female (LACM); ibidem, 1–14.xi.1997, 1 female (LACM); Monte Negro, Fazenda Amorim (10.6683 S, 63.4833 W), 03–15.xii.2011, Amorim, Ament & Riccardi *leg*., 1 female (MZSP); Porto Velho, AHE Jirau, Rio Madeira (9.5981 S, 65.3667 W), 28.iii–08.iv.2011, R. R. Silva, E. Z. Albuquerque & eq. *leg*., 1 female (MZSP). Roraima: Ilha de Maracá, Rio Uraricoera, 19–24.vii.1987, J. A. Rafael & L. S. Aquino *leg.*, 1 female (Det.: A. Norrbom, 1990) (INPA); Pacaraima, 5–8.iii.1988, Eq. J. A. Rafael *leg*., 1 female (INPA). BOLIVIA: Sta Cruz, Buena Vista, 21.ii.1999, F. D. Parker *leg*., 1 female

(LACM). COLOMBIA: Antioquia: Mpio la Pintada, Farailon La Paz, 16.ii.2007, N. Uribe *leg.*, 1 male (CEUA); idem, Sán Jerónimo, Parque los Tamarindos, 425 m, 24–27.iv.2006, A. Velez *leg.*, 1 male (CEUA 38267); idem, San Roque vrd, El Topacio, VSR Rez Bosque F1, v.2013, 1 male (CEUA); Ma, Santa Marta, Puerto Mosquito Rva La Iguana Verde, bosque VSR (11.1852 N, 74.1769 W), 09.xi.2012, C. Valverde *leg*., 1 male (CEUA); ibidem, 10.xi.2012, 1 male (CEUA). Santander: Cimitarra, Ciénaga de Cachimberos, Hacienda San Miguel, 05–8.x.2001, M. Castaño & M. Velez *leg*., 2 males (CEUA 38268); idem, Hacienda El Bosque, Campamento Ecuador, Bosque Ecuador, 09–12.x.2001, 1 male (CEUA 38133); idem, Vd. Primavera, 05–8.v.2001, M. Castaño & M. Velez *leg.*, 3 males (CEUA 38269); idem, Vereda Primavera Km 4, Hacienda El Bosque, Campamento Santa Isabel, 01–4.x.2001, 1 male (CEUA 38270); San J. Girón, Prof. Sogamoso Denso Tierra, 603 m, 10–11.v.2015, Y. Correa *leg*., 1 male (CEUA). COSTA RICA: Alajuela: 2 Km S Pital, 05–28.ix.1988, F. D. Parker *leg*., 1 female (LACM); 20 Km S Upala, 14–17.viii.1990, F. D. Parker *leg*., 1 female (EMUS); ibidem, 21–23.viii.1990, 1 female (EMUS); ibidem, 28–30.viii.1990, 2 females (EMUS); ibidem, 01–10.v.1990, 1 female (LACM); ibidem, vi.1990, 2 females (LACM); ibidem, 15.vii.1990, 1 female (LACM); ibidem, 29.vii.1990, 1 female (LACM); ibidem, 01.viii.1990, 1 male (LACM); ibidem, 07–09.viii.1990, 1 female (LACM); ibidem, 21–23.viii.1990, 2 females (LACM); ibidem, 28–30.viii.1990, 1 female (LACM); ibidem, 10–13.ix.1990, 1 female (LACM); ibidem, 16–25.ix.1990, 1 female (LACM); ibidem, 27.ix–18.x.1990, 1 male and 2 females (LACM); ibidem, 1–5.x.1990, 1 female (LACM); ibidem, 16.x.1990, 3 females (LACM); ibidem, 23.x.1990, 4 females (LACM); ibidem, 26–30.x.1990, 2 females (LACM); ibidem, 28.x.1990, 4 females (LACM); ibidem, 30.x.1990, 3 females (LACM); ibidem, 01.xi.1990, 7 females (LACM); ibidem, 01–20.xi.1990, 2 females (LACM); ibidem, 06.xi.1990, 5 females (LACM); ibidem, 8.xi.1990, 11 females (LACM); ibidem, 13.xi.1990, 7 females (LACM); ibidem, 20.xi.1990, 3 females (LACM); ibidem, 29.xi.1990, 3 females (LACM); ibidem, 06.xii.1990, 4 females (LACM); ibidem, 11.xii.1990, 3 females (LACM); ibidem, 13.xii.1990, 1 female (LACM); ibidem, 13.xii.1990–09.i.1991, 2 males (LACM); ibidem, 06.i.1991, 1 male (LACM); ibidem, 20.i–12.ii.1991, 1 male (LACM); ibidem, 29.i.1991, 2 females (LACM); ibidem, 05.ii.1991, 2 females (LACM); ibidem, 07.ii.1991, 1 female (LACM);

ibidem, 12.ii–05.iii.1991, 1 female (LACM); ibidem, 3–9.iii.1991, 1 male and 1 female (LACM); ibidem, 05–18.viii.1991, 1 male (LACM); ibidem, 10–19.iii.1991, 3 females (LACM); ibidem, 12.iii.1991, 2 females (LACM); ibidem, 18–26.iii.1991, 1 female (LACM); ibidem, 20–26.iii.1991, 2 females (LACM); ibidem, 27–31.iii.1991, 5 females (LACM); ibidem, 1–10.iv.1991, 6 females (LACM); ibidem, 11–20.iv.1991, 2 females (LACM); ibidem, 12–30.iv.1991, 1 female (LACM); ibidem, 1–9.v.1991, 1 female (LACM); ibidem, 10–21.v.1991, 2 females (LACM); ibidem, 1–11.vi.1991, 1 female (LACM); ibidem, 03.vi.1991, 1 female (LACM); ibidem, 07.vi.1991, 1 female (LACM); ibidem, 21.vi.1991, 1 female (LACM); ibidem, 1–15.vii.1991, 1 female (LACM); ibidem, 16–24.vii.1991, 4 females (LACM); ibidem, 21–31.vii.1991, 2 females (LACM); ibidem, 1–10.x.1991, 1 female (LACM); ibidem, 11–21.x.1991, 1 female (LACM); ibidem, 22–31.x.1991, 1 female (LACM); Golfito: 22.vii.1957, Truxal & Menke *leg*., 2 females (Det.: Korneyev & Kameneva, 2001, Det.: Kameneva, 2001) (LACM); ibidem, 24.vii.1957, 1 male (LACM). Guanacaste: S Cañas, 11–15.iii.1989, F. D. Parker *leg*., 1 male (LACM); 14 Km S Cañas, 14–16.x.1989, F. D. Parker *leg*., 1 male (LACM); ibidem, 15–25.vii.1990, 1 female (LACM); ibidem, 24–31.viii.1990, 2 females (LACM); ibidem, 16–19.xi.1990, 1 female (LACM); ibidem, 1–22.vi.1991, 1 female (LACM); 3 Km SE R. Naranjo (10.7911 N, 85.6689 W), 15–22.x.1991, F. D. Parker *leg*., 1 female (LACM); ibidem, 20.xi.1991, 1 male (LACM); ibidem, 1–5.xii.1991, 1 female (LACM); ibidem, 10–23.i.1992, 1 female (LACM); ibidem, 20–31.i.1992, 1 female (LACM); ibidem, 10–19.ii.1992, 1 female (LACM); ibidem, 23–31.viii.1992, 1 female (LACM); ibidem, iv.1992, 1 female (LACM); ibidem, v.1992, 1 female (LACM); ibidem, 13.vii.1992, 1 female (LACM); ibidem, 10–20.ix.1992, 1 male (LACM); ibidem, 11–20.ix.1992, 1 male (EMUS); ibidem, 1–9.x.1992, 1 female (LACM); ibidem, 22.x.1992, 1 female (LACM); ibidem, xii.1992, 1 female (LACM); ibidem, 4–8.i.1993, 1 female (LACM); ibidem, 15–19.iii.1993, 1 male (LACM); ibidem, 15–30.iv.1993, 1 female (LACM); ibidem, 1–9.vii.1993, 1 female (LACM); ibidem, 14–16.vii.1993, 1 female (LACM); ibidem, 1–3.vii.1993, 1 female (LACM); ibidem, 25.vii.1993, 1 female (LACM); ibidem, 23.viii.1993, 1 female (LACM). Heredia: La Selva (10.4333 N, 84.0167 W), 06.ix.1999, INBio-OET, 1 female (LACM); ibidem, 10.ix–03.x.1999, 1 female (LACM); ibidem, 20.ix.1999, 3 females (LACM); La Selva Res. Sta., 24–

30.viii.1988, W. J. Hanson *leg*., 1 female (LACM). Higuito: San Mateo CR, Pablo Schild *leg*., 1 male (USNM). Limon: 7 mi N Guacimo, 22.ii–3.iii.1988, F. D. Parker *leg*., 1 female (LACM); Prov. Guapiles, 25.vi.1965, R. J. Hamton *leg*., 1 male (LACM). Puntarenas: Piedras Blancas 24 Km W (8.7833 N, 83.2500 W), 200 m, xi.1990, P. Hanson *leg.*, 1 female (Det.: Kameneva, 2001) (USNM). San Jose: Escazu, 19–24.iv.1988, F. D. Parker *leg*., 1 female (LACM); ibidem, 15–22.vii.1989, 1 female (LACM); ibidem, 23–24.ix.1989, 1 female (LACM); San Isidro 9 mi S (9.331 N, 83.6993 W), 31.xii.1988, F. D. Parker *leg*., 1 female (EMUS). Turrialba: Catie/IICA Research Station, 24–30.vii.1981, W. R. Dolling B. M. 1981–411, 1 male (NHMUK 010862541). ECUADOR: Napo: Lago Agrio 8 Km W, 28.viii.1975, Langley & Cohen *leg*., 1 female (USNM); Limoncocha, 15.vi.1977, P. J. Spangler & D. R. Givens *leg.*, 3 females (USNM); Misahualli nr. Tena, 6–19.x.2001, C. Brammer *leg*., 1 male (LACM); Res. Ethnica Waorani 1 Km S, Onkone Gare Camp (0.6527 S, 76.4333 W), 03.vii.1995, T. L. Erwin et al. *leg.*, 1 female (USNM); ibidem, 26.vi.1996, 1 male (USNM); ibidem, 08.ii.1996, 1 male (Det.: V. Korneyev, 2008) (USNM); Yasuni Res. Sta. (0.6667 S, 76.3833 W), 250 m, 19–30.x.1998, W. J. Hanson *leg*., 8 females (LACM). Sucumbios: Sacha Lodge (0.5000 S, 76.4833 W), 270 m, 20–30.ix.1994, P. Hibbs *leg*., 1 female (LACM). EL SALVADOR: El Impossible, 04.vii.1977, Jarger *leg.*, 1 female (USNM). La Unión (13.3351 N, 87.8470 W), 25.i.1957, P.A.B *leg.*, 1 male (USNM); idem, 25.i.1957, G.R.S. *leg.*, 2 females (USNM). Santa Tecla, 23.ii.1935, P.A.B. *leg.*, 1 male (USNM). GUATEMALA: Escuintla: Palín, 1992, J. Lopez *leg.*, 1 male and 1 female (Det.: A. Norrbom, 1992) (USNM). Rodriguez, 1 male (Det.: E. E. Austen, 8.ix.1926: *Stylophthalmyia fascipennis* Frey) (NHMUK 010862536). Sta. Lucia Cotz., 02–11.v.1988, F. D. Parker *leg*., 1 female (LACM). HONDURAS: Atlántida, La Ceiba, 07.ix.1916, F. J. Dyer *leg*., 1 female (USNM). MEXICO: Chiapas: Cacahoatan, 30.viii.1967, H. Sanchez R. *leg.*, 2 females (USNM); Tuxtla Chico, 02.viii.1967, H. Sanchez R. *leg.*, 1 male (USNM). Sinaloa, 68 mi SE Culiacan, 23.iv.1977, Hanson & Davis *leg*., 1 female (LACM). NICARAGUA: Masaya: La Concha, Estrada 62–2376, 02.vii.1961, Sequeira & Leal *leg.*, 2 males (USNM). PANAMA: Barro Colorado: CZ, iv–v.1937, J. Zetek *leg*., 1 female (USNM); ibidem, vii.1937, 3 females (USNM); ibidem, x–xi.1941, 1 female (USNM); ibidem, i–iii.1944, 2 males and 2 females (USNM); Canal

Zone, 09.vii.1978, N. E. Woodley *leg*., 1 female (Det.: *Terpnomyia* sp. G. Steyskal, 1982) (USNM); ibidem, 14.vii.1978, 1 female (USNM); Is, xi.1937, J. Zetek *leg.*, 2 females (USNM); idem, 10–17.v.1964, W. D. & S. S. Duckworth *leg.*, 1 male (USNM); idem, 25–28.iii.1965, S. S. & W. D. Duckworth *leg*., 1 female (USNM). Cerro Campana, 11–14.vii.1967, O. S. Flint, Jr. *leg.*, 1 female (USNM). El Cermeño, iv–v.1939, 1 female (USNM); idem, xii.1939–i.1940, J. Zetek *leg.*, 2 males and 1 female (USNM). La Campana, i–iii.1938, J. Zetek *leg.*, 1 male and 3 females (USNM). PERU: Dp. Junin: Chanchamayo, 11.viii.1918, J. M. Schunke *leg.*, 1 female (USNM). Huanuco: Cochicote, 08.ix.1965, J. C. Hitchcock, Jr. *leg.*, 1 female (Det.: G. Steyskal, 1965) (USNM); vic. Tingo Maria, 1–5.vi.1999, W. Hanson & S. Keller *leg*., 2 females (LACM). Iquitos, iii–iv.1932, R. C. Shannon *leg.*, 1 female (Det.: Greene: *Terpnomyia latifrons* Hendel) (USNM). TRINIDAD: Simla, Arima-Blanchisseuse Rd., 20.vii.1975, J. Price *leg.*, 1 male (USNM); Simla Res. Sta., I., 2–15.vi.1981, Hanson & Clemons *leg*., 1 male and 6 females (LACM). VENEZUELA: Lara, 4 Km NW de La Pastora, 2–3.iii.1978, J. B. Heppner *leg.*, 1 male (USNM). T. F. Amaz., Cerro de La Neblina Basecamp (0.8333 N, 66.1622 W), 140 m, 4–12.ii.1984, D. Davis & T. McCabe *leg.*, 2 females (USNM); ibidem, 1–10.iii.1984, 1 female (USNM).

Distribution. Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Venezuela, Trinidad, Colombia, Ecuador, Peru, Bolivia and Brazil (Amazonas and Pará). New records: Belize and Brazil (Acre, Rondônia, Roraima, Amapá and Maranhão) (Fig. 26).

Comments. A female specimen from the locality "Paraguay: Depto Alto Paraguay, 14–16.04.1986, Pague, Solis *leg.* (USNM)" was analyzed and identified by Kameneva (2004b) as *P. latifrons*. However, from the analysis of this specimen, it was concluded that it belongs to the genus *Pterocerina*.

Plagiocephalus intermedius Kameneva, 2004
(Figs.19E, 21G–I, 22E–F)

Plagiocephalus intermedius: Kameneva, 2004b: 19 (Holotype: 1 male, INBio; Paratypes: 3 males and 17 females, INBio) (examined by photographs).

Type material. Holotype (male): Costa Rica: Puntarenas: Monteverde, San Luis, Buen Amigo, 1000–1350 m, ix.1994, 3224 (Fuentes) (Fig. 19E). Paratypes (3 males, 17 females): Costa Rica: Cartago: A. C. Amistad, P. N. Tapanti, 1150 m, i.1994, male (Mora); Guanacaste: Rio San Lorenzo, Tierras Morenas, Z. P. Tenorio, 1050 m, i.1993, female (Rodriguez); P. N. Guanacaste: Est. Cacao, vii.1989, female (GNP Biod. Sur.); ibidem, SW side Volcan Cacao, 1000–1400 m, xi–xii.1989, female (Blanco, Chaves); ibidem, Lado SO Volcan Cacao, 800–1600 m, 12–17.vii.1993, female (Fuentes); Puntarenas: Monteverde, San Luis, Buen Amigo, 100–1350 m, ix.1994, female; ibidem, xi.1994, male; ibidem, 25.xi–10.xii.1996, male (Fuentes); Est. Pittier, Sendero Pittier, 1670 m, 26.vi.1995, female (Angulo); ibidem, 21.vi–4.vii.1995, 2 females (Moraga); ibidem, 25.vi–4.vii.1995, 3 females (Zumbado); ibidem, 1700 m, 3.vii.1995, 2 females (Zumbado); Buenos Aires, Est. Altamira, Sendero Los Gigantes, 1450 m, 4.i–3.ii.2000, 4 females (Rubi) (INBio).

Diagnosis. *Plagiocephalus intermedius* can be differentiated by eyestalks of male longer than in *P. lobularis* and shorter than in *P. latifrons* (3.00–7.00 mm); female parafacialia yellow (Fig. 21G); radial-medial band with base wider than apex and at most barely touching the discal band (Figs. 22E, F). The species can also be distinguished by male face yellowish white; male scape, pedicel and first flagellomere entirely yellow, and female scape, pedicel and first flagellomere gold with apex darker (Fig. 21G); palpus yellow (Fig. 21G); proboscis reddish yellow with brown and yellow setulae. Male wing of normal outline, without posterior lobes (Fig. 22E); vein r-m located before vein R_1 apex (Figs. 22E, F); male subapical band curved and narrower when touching the anterior apical band (Fig. 22E); male anterior apical band wider than in *P. lobularis* and *P. latifrons* (Fig. 22E). Male fore and mid leg entirely yellow, and hind leg yellow to gold; female legs brown with tarsi lighter, and fore femur yellowish on the apex (Fig. 21I).
Measurements: Male: body (4.50–5.80 mm); wing (4.70–6.10 mm). Female: body (2.88–3.35 mm); wing (4.62–5.7 mm); oviscape (1.29–1.50 mm).

Examined material. COSTA RICA: La Suiza, 1961, P. Schild *leg*., 1 female (USNM); idem, 24.xi.1961, PablSchild *leg*., 1 female (USNM).

Distribution. Costa Rica (Fig. 27).

Comments. Part of the INBio collection, including the material type of *P. intermedius*, was aggregated to the Museo Nacional de Costa Rica. The material of *P. intermedius* analyzed had been previously analyzed and misidentified as *P. latifrons* by Kameneva (2004b).

DISCUSSION

Phylogenetic hypothesis of Pterocallini

The trees generated by the analysis under implied weighting (Figs. 12–16) presented a better resolution in topologies than the analysis under equal weighting (Fig. 11). The consensus tree generated by the parsimony analysis under equal weighting corroborated five major clades: (1) (*Paragorgopsis* + *Plagiocephalus*); (2) (*Chondrometopum* + *Cymatosus* + *Megalaemyia*); (3) (*Pseudopterocalla* + *Xanthacrona*); (4) (*Paragorgopis euryale* (*Neoacanthoneura*)); (5) (*Pterocerina* sp. 4 (*Pterocerina nigripes* (*Pterocerina paradoxa* (*Pterocerina colorata* (*Pterocerina* sp. 1 (*Pterocerina* sp. 2 + *Pterocerina* sp. 3)))) + (*Apterocerina* sp. 1 (*Pterocerina rificauda* (*Apterocerina* sp. 2 (*Cyrtomostoma* + *Tetrapleura*) + (*Lathrostigma* + *Aciuroides*)))))). *Bothrometopa*, *Dasymetopa*, *Megalaemyia costalis* Hendel, 1909, *Terpnomyennis*, *Rhyparella*, *Terpnomyia*, *Neomyennis* and *Pterocalla* did not form a clade with any other genus in the analysis under equal weighting.

The use of different weighting in the search of trees allowed the identification of the most stable and least stable clades in the topologies. The five topologically distinct trees that resulted from the analysis under different weights recovered some common clades (Figs. 12–16). *Terpnomyennis* formed a sister group with *Terpnomyia* in all the analysis under implied weighting. A clade composed of *Rhyparella*, *Dasymetopa*, *Megalaemyia*, *Cymatosus* and *Chondrometopum* was also recovered in all analysis under implied weighting, but the relationship among the species differed among the topologies. *Paragorgopis euryale* Kameneva, 2004 forming the sister group of *Neoachantoneura* was recovered in all phylogenetic analysis under implied weighting. The last monophyletic group that appeared in all the analysis under implied weighting was the clade formed by *Pterocerina*, *Apterocerina*, *Tetrapleura*, *Cyrtomostoma*, *Lathrostigma* and *Aciuroides*. The relationship among the last genera also varied, with exception of *Lathrostigma* and *Aciuroides*, which were recovered as sister groups in all the topologies. The genera that most varied in position among the trees are *Bothrometopa*, *Neomyennis*, *Pseudopterocalla*, *Pterocalla* and *Xanthacrona*.

The choice of the preferred tree was made based on the number of steps, IC, IR and number of resulted trees. The trees resulted from the analysis using $14 \leq k \leq 30$

presented one less step than the analysis with $10 \leq k \leq 13$, but equal IC and IR (Table 2). However, this analysis produced six most parsimonious trees, which are less desirable than one resulting tree as an explanatory hypothesis of the data. The parsimony analysis under implied weighting with $k = 10–13$ resulted in one most parsimonious tree with 492 steps, IC of 29 and IR of 68. This tree was chosen as the main hypothesis of relationship among the genera of Pterocallini and is the topology in which the discussion is going to be based on.

The clade A is formed by *Terpnomyennis* and *Terpnomyia*, and sustained by a homoplastic synapomorphy: the ocellar triangle positioned anteriorly to the inner vertical setae (character 2, state 1) (Fig. 17 (part I)). Kameneva (2004a) mentioned a close relationship between *Terpnomyennis* and *Terpnomyia*, since both genera are almost identical in the shape of the head. Kameneva (2004a) also hypothesized that *Tepnomyennis* would be positioned basally in a phylogeny because the unmodified states compared to the ground plan of Tephritoidea, and presence of setae on the sternite 6 of the females. However, this clade had a low support in the analysis (Fig. 18).

The clade B is composed of *Xanthacrona* species, and supported, respectively, by one synapomorphy and three homoplastic synapomorphies: scutellum swollen (character 29, state 0), crossvein r-m in relation to cell dm positioned in the third apical of the cell (character 47, state 2), absence of posterior lobe of cell cup (character 52, state 1) and eversible membrane with denticles organized like scales (character 66, state 0) (Fig. 17 (part I)). The analysis included all the species of *Xanthacrona* and sustained the monophyly of the genus with high Relative Bremer support (Fig. 18). *Xanthacrona* is easily recognized by the species with yellowish coloration, unique band pattern on the wing and modifications in the shape of the scutellum. The most enigmatic species of Pterocallini is belonged to *Xanthacrona*: *X. phyllochaeta*. This species present lanceolate setae on the head and thorax of both sexes, presence of presutural setae on the thorax, which is not present in any other Pterocallini, presence of glans in the apex of distiphallus, which is a character only present in other tribes of Ulidiidae, such as Ulidiini, and absence of presinsetae in the medial surstylus. The identification of *X. phyllochaeta* was confirmed by photos of the type, but the real identity of this species

might not be solved yet. *Xanthacrona phyllochaeta* may belong to another tribe of Ulidiidae seeing that it possess characters absent in the species of Pterocallini.

The clade C is formed by *Pterocalla* and is sustained, respectively, by one exclusive synapomorphy and three homoplastic synapomorphies: scutum with no microtrichia at bases of setulae (character 22, state 1), ocellar setae distinctly shorter than the postocellar setae (character 3, state 0), scutellum triangular shaped (character 26, state 1) and vein CuA_1 not reaching the posterior margin of the wing (character 51, state 1) (Fig. 17 (part I)). *Pterocalla* is the second largest genus of Pterocallini with 19 described species, but only three species were sampled in the analysis. However, the type species of *Pterocalla*, *P. ocellata* (Fabricius, 1805), was included and formed a monophyletic group with the other two species. This genus is commonly found in field expeditions and the species are easily recognized by the peculiar wing pattern (Fig. 7N).

The clade D is composed of *Bothrometopa*, *Pseudopterocalla* and *Neomyennis* (Fig. 17 (part I)). The monophyly of the group is sustained by one homoplastic synapomorphy: presence of two supra-alar setae (character 23, state 1) (Fig. 17 (part I)). *Bothrometopa* is a monotypic genus, *Pseudopterocalla* has two and *Neomyennis* has three species described. The monophyly of *Pseudopterocalla* and *Neomyennis* was corroborated by the phylogenetic analysis with maximum support. *Pseudopterocalla* was treated as a subgenus of *Pterocalla* by some authors because of the similarity of the wing patterns between these two genera (Hendel 1909b, Steyskal 1982). However, the analysis revealed that *Pseudopterocalla* and *Pterocalla* are not closely related.

The clade E is formed by *Paragorgopis* and *Plagiocephalus*, and is supported by four homoplastic synapomorphies: gena higher than half the height of the eye (character 11, state 2), clypeus shorter than the diameter of the scape (character 19, state 0), oviscape two times longer than wide (character 62, state 2) and presinsetae with inner surface serrated (character 82, state 0) (Fig. 17 (part II)). Both genera are similar in having the male head wider than the female in *Plagiocephalus* and in some of the species of *Paragorgopis*. Kameneva (2004a) divided *Paragorgopis* into two groups: the group of species related to the type species, *P. maculata* Giglio-Tos, 1893, and the group of species related to *P. mallea* Hendel, 1909. The species that compose the clade E is

formed by species from the last group, which are mainly characterized by the wing with hyaline spots with rounded dark spots inside (Fig. 7L).

The *Plagiocephalus* node was recovered in the analysis with a very high support of the Relative Bremer index (Fig. 18), and support of five synapomorphies, such as male head extremely transverse (character 0, state 2) and vein R_{2+3} almost straight (character 46, state 1), and 12 homoplastic synapomorphies (Fig. 17 (part II)). Even though *Plagiocephalus* being a very unique genus of Pterocallini with several autapomorphies recognized in the species, the time spending on studies of the morphology of *Plagiocephalus* certainly influenced the analysis by sustaining the genus with a high support of synapomorphic characters. *Plagiocephalus* was corroborated as a monophyletic group, but the possible sister groups of the genus need to be more explored, since the analysis reconstructed the relationship between *Paragorgopis* and *Plagiocephalus* with a very low support (Fig. 18).

The clade F is constituted of *Rhyparella*, *Megalaemyia*, *Dasymetopa*, *Cymatosus* and *Chondrometopum*, and is supported by three homoplastic synapomorphies: face in lateral view straight (character 17, state 0), scutum with microtrichia uniformly distributed (character 22, state 3) and distiphallus about the same length of the abdomen (character 88, state 1) (Fig. 17 (part II)). Kameneva (2004a) transferred *Rhyparella novempunctata* Hendel, 1909 to *Dasymetopa*, and now, *Rhyparella* has only one species belonging to the genus. Kameneva (2004a) pointed out *Dasymetopa* as a possible paraphyletic or polyphyletic group, since the characteristics that define the genus are very loosely. Some of the species of *Dasymetopa* are easily recognized by the broad head of the male. *Megalaemyia* was not recovered as a clade in the analysis. The dubious concept of *Megalaemyia* had been noticed by Kameneva (2009), which commented that the genus is probably paraphyletic or polyphyletic. *M. costalis* Hendel, 1909a was recovered as sister group of (*Dasymetopa* + *Cymatosus* (*Chondrometopum* + *Megalaemyia)*. In fact, *M. costalis* is not morphologically similar to the other species of *Megalaemyia* and probably is going to be transferred to another genus in a future revision. Kameneva (2009) indicated that *Megalaemyia* and *Cymatosus* are closely related by discussing some of the synapomorphies shared by these two genera, such as the head shape, vein R_1 bare and dipped posteriorly before the apex, and epandrium short oval with two distantly

separated presinsetae. *Cymatosus* is rarely found in collections and, before, only 25 specimens of the genus were known (Kameneva 2009). *Chondrometopum* is a remarkable genus for the modifications in the shape of the head. The male of *Chondrometopum bifinestratum* Kertész, 1913 has a horn-like process at the corners of the gena (Kameneva 2004a). Kameneva (2004a) mentioned a possible close relationship between *Chondrometopum* and *Dasymetopa stigma* Hendel, 1909a, but they were not recovered in the analysis as sister groups. The clade composed of *Cymatosus*, *Chondrometopum* and part of the *Megalaemyia* were sustained with high support (Fig. 18).

The clade G, composed of *Paragorgopis euryale* and *Neoacanthoneura*, was established with relatively low support (Fig. 18). The monophyly of the clade is defined by the setae in the frons (character 8, state 0) and absence of tegument extension in the mid-apical portion of the oviscape (character 63, state 1), which are non-exclusive synapomorphies. *P. euryale* belongs to the group of species of *P. maculata*, in which the species are mainly recognized by the wings with rounded hyaline spots without dark dots inside (Fig. 7K). *Paragorgopis* is a polyphyletic group that appeared in the tree in two phylogenetic distant clades (E and G). The groups of species of *P. maculata* and *P. mallea* should be separated in two distinctive genera. *Neoacanthoneura* is one of the few genera of Pterocallini that were taxonomicaly revised (Kameneva 2012). Kameneva (2012) described 11 new species, almost the total of species recognized in the genus (12), and divided *Neoacanthoneura* into two groups of species: *apicalis* and *euphrantina*. *Neoacanthoneura brachioptera* Kameneva, 2012 and *Neoacanthoneura* sp. 1 belong to the *apicalis* group of species, mainly characterized by the wing with a dark brown pattern of three crossbands. In most species of this group, the male wing is modified in the shape and the costal vein is covered by dentate setae (Kameneva 2012). *Neoacanthoneura* sp. 2 belongs to the *euphrantina* group of species, which is characterized by the wing mostly brown with hyaline spots and incisions, similar to the wing of the group of species of *P. maculata*.

The clade H is composed of six genera: *Pterocerina*, *Apterocerina*, *Cyrtomostoma*, *Tetrapleura*, *Lathrostigma* and *Aciuroides*. This clade is strongly supported by five exclusive and seven non-exclusive synapomorphies. The exclusive synapomorphies that sustained its monophyly are the presence of setulae in the

anepimerum (character 33, state 0), vein R_1 entirely setulose (character 38, state 2), eversible membrane of the female terminalia with pointed denticles (character 67, state 2), segment 8 of the female terminalia about the same diameter of the hind tarsus (character 68, state 1) and cerci of the female terminalia flattened (character 70, state 1). Three of the five synapomorphies that sustained the clade H are from the female terminalia. The distinctive ovipositor of most of the species of the clade H is characterized by the flattened and wide segment 8, and acute apex of the cerci. Presumably, these specializations are a strategy of oviposition in harder surfaces, for example, plants with a thicker layer of cuticle. The close relationship among the genera of the clade H has been hypothesized by Kameneva (2012), who also listed the synapomorphies that indicates that these groups are closely related, such as lower orbital setae at the middle of frons, cell cup closed by an arcuate vein and segment 8 rigid and flattened. The phylogenetic analysis indicated *Pterocerina* and *Apterocerina* as non-monophyletic genera. *Pterocerina* is the largest genus of Pterocallini, with 29 described species. However, *Pterocerina* has not been taxonomically revised and there is no key for identification of the species of the genus. *Cyrtomostoma*, *Tetrapleura* are *Lathrostigma* are monotypic genera. *Aciuroides*, which has two described species, was revised by Kameneva (2012).

Coscinum, *Elapata*, *Goniaeola*, *Micropterocerus*, *Ophthalmoptera* and *Parophthalmoptera* were not included in the phylogeny presented in this work. However, some assumptions can be made in relation to the phylogenetic position of these groups. As already commented by Kameneva (2012), *Coscinum*, *Elapata* and *Microptetocerus* share some characters with *Aciuroides, Apterocerina*, *Cyrtomostoma*, *Lathrostigma, Pterocerina* and *Tetrapleura*, thus, these genera possibly belong to the clade H of the present hypothesis. *Parophthalmoptera*, because of similarities in the head shape and wing spot pattern with *Megalaemyia*, probably has a close relationship with the clade F (Kameneva & Korneyev 2010). Suppositions about the phylogenetic placement of *Goniaeola* and *Ophthalmoptera* in the phylogeny of Pterocallini are very speculative, but because of many morphological disparities, these genera could not belong to the clade H of the phylogeny.

The clade formed by all of the Pterocallini is sustained by two exclusive synapomorphies, palpus not broad (character 20, state 0) and oviscape 1.5 longer than wide (character 62, state 1), and three non-exclusive synapomophies. The Relative Bremer Support of the clade was relatively high (Fig. 18), but the analysis did not aim to test the monophyly of the tribe. Therefore, a phylogenetic hypothesis with broad approach of the family should be made for testing the validity of every tribe of Ulidiidae. As the knowledge on Pterocallini is still very incipient, any assumption on biogeography and distribution of the taxa could not be made. However, apparently most of the species of Pterocallini are widely distributed in the Neotropics, with some species of the same genus occurring sympatrically and other with disjunctive distribution, for example, *Plagiocephalus latifrons* and *P. lobularis* (Fig. 24).

CONCLUSIONS

This study was the first to attempt to propose a hypothesis of internal phylogenetic relationship of Pterocallini. The phylogenetic analysis corroborated the monophyly of most of the genera analyzed. The non-monotypic *Aciuroides*, *Plagiocephalus*, *Pseudopterocalla* and *Xanthacrona* had all the species included in the analysis and were recovered as monophyletic. *Lathrostigma*, *Rhyparella* and *Terpnomyia*, which are monotypic, but had new species included in the phylogenetic analysis, had their monophyly supported. The analysis also indicates the monophyly of *Neomyennis* and *Pterocalla*. The monophyly of *Chondrometopum*, *Cymatosus* and *Neoacanthoneura* remains inconclusive. The phylogeny indicated *Dasymetopa* as monophyletic, but because of the lack of synapomorphies in the genus and the unsatisfactory sample of species in the analysis, its monophyly remains uncertain and deserves to be reassessed hereafter. Most of the genera of Pterocallini are poorly studied, but especially *Paragorgopis*, *Megalaemyia*, *Apterocerina* and *Pterocerina*, which did not have their monophyly corroborated, are the priority genera for future taxonomic revisions.

The concept of *Plagiocephalus* includes three species easily recognized. The monophyly of the genus was corroborated with strong support in the analysis. New records of distribution of the species updated the known distribution of the genus, and new characters of the terminalia of *Plagiocephalus* contributed with the positioning of the genus within Pterocallini.

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TABLES

Table 1. Taxa sampling in the phylogenetic inference of relationship of Pterocallini.

Genus	Total number of described species	Number of species utilized in the morphological analysis
Aciuroides	2	2
Apterocerina	5	2
Bothrometopa	1	1
Chondrometopum	3	1 undescribed
Cymatosus	4	1
Cyrtomostoma	1	1
Dasymetopa	12	3
Lathrostigma	1	1 + 1 undescribed
Megalaemyia	5	4 + 1 undescribed
Neoacanthoneura	12	1 + 2 undescribed
Neomyennis	3	2
Paragorgopis	11	4
Plagiocephalus	3	3
Pseudopterocalla	2	2
Pterocalla	19	3
Pterocerina	29	8
Rhyparella	1	1 + 1 undescribed
Terpnomyennis	1	1
Terpnomyia	1	1 + 1 undescribed
Tetrapleura	1	1
Xanthacrona	5	5

Table 2. Values of the constant of concavity (*k*) applied in the analysis with implied weighting with their respective number of steps (L), consistency index (IC), retention index (IR), *fit* value and number of trees generated.

k	L	IC	IR	*fit*	# trees
1	517	28	66	54.41274	1
2	500	29	67	45.46035	1
3	500	29	67	39.41458	1
4	500	29	67	34.97567	1
5	500	29	67	31.52856	1
6	495	29	68	28.74367	1
7	495	29	68	26.42370	1
8	495	29	68	24.46950	1
9	495	29	68	22.79719	1
10	492	29	68	21.34652	1
11	492	29	68	20.06700	1
12	492	29	68	18.93677	1
13	492	29	68	17.93046	1
14	491	29	68	17.02800	6
15	491	29	68	16.21281	6
20	491	29	68	13.09437	6
30	491	29	68	9.47470	6

FIGURES

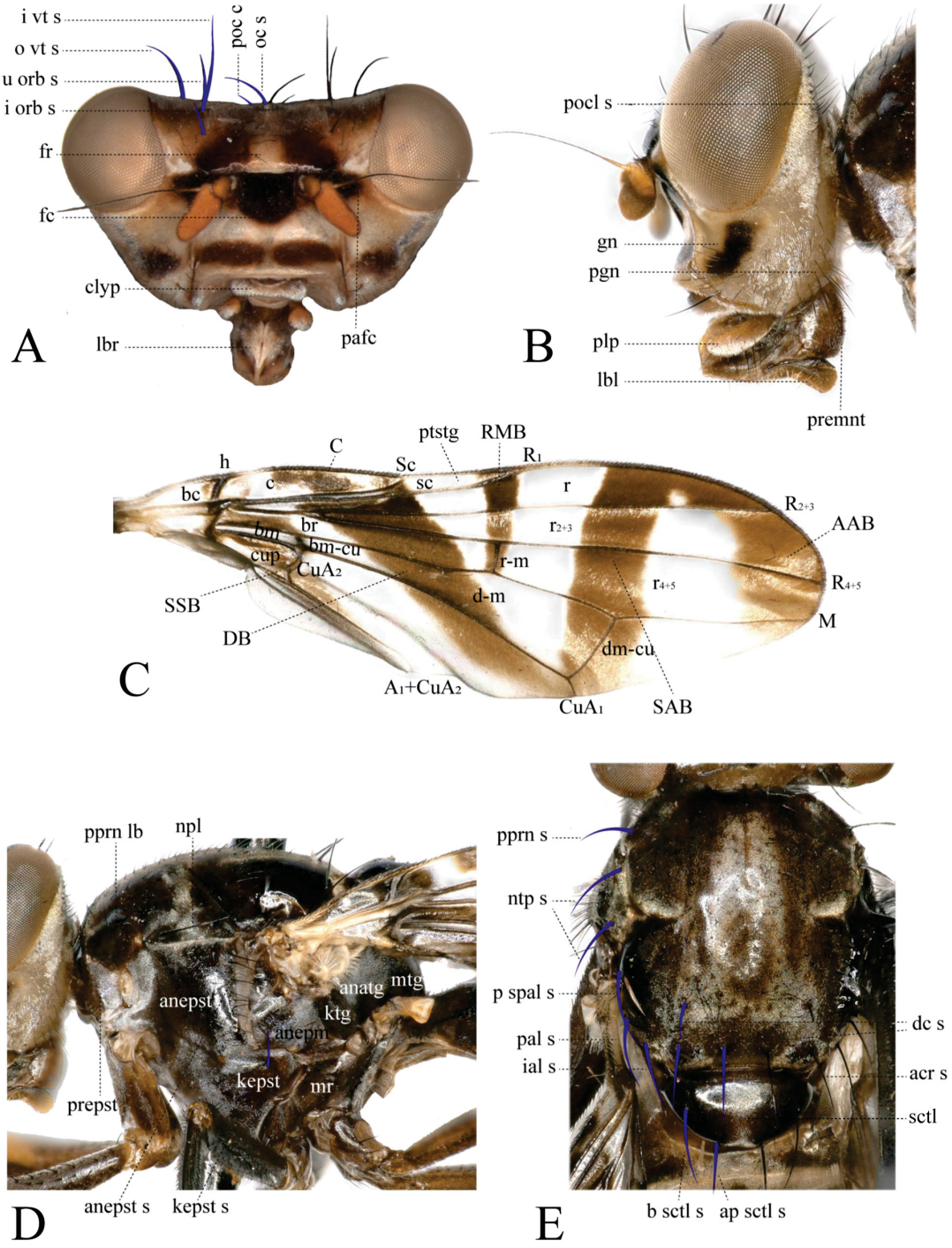


Figure 1. A–E. External morphology (*Plagiocephalus latifrons* (female)): A. Frontal view of the head; B. Lateral view of the head; C. Wing; D. Lateral view of the thorax; E. Dorsal view of the thorax. Abbreviations: acr s, acrostichal seta; anatg, anatergite; anepm, anepimerum; anepst s, anepisternal setae; anepst, anepisternum; ap sctl s, apical scutellar seta; b sctl s, basal scutellar seta; clyp, clypeus; dc s,

dorsocentral seta; fc, face; fr, frons; gn, gena; i vt s, inner vertical seta; ial s, intra-alar seta; kepst s, katepisternal seta; kepst, katepisternum; ktg, katatergite; lbl, labella; lbr, labrum; l orb s, lower orbital seta; mr, meron; mtg, mediotergite; npl s, notopleural setae; npl, notopleuron; oc s, ocellar seta; o vt s, outer vertical seta; p spal s, posterior supra-alar seta; pafc, parafacialia; pal s, postalar seta; pgn, postgena; plp, palpus; poc s, postocellar seta; pocl s, postocular seta; pprn lb, postpronotal lobe; pprn s, postpronotal seta; premnt, prementum; prepst, proespisternum; ptstg, pterostigma; sctl, scutellum; u orb s, upper orbital seta. Wing pattern abbreviations: AAB, anterior apical band; DB, discal band; RMB, radial-medial band; SAB, subapical band; SBB, subbasal band.

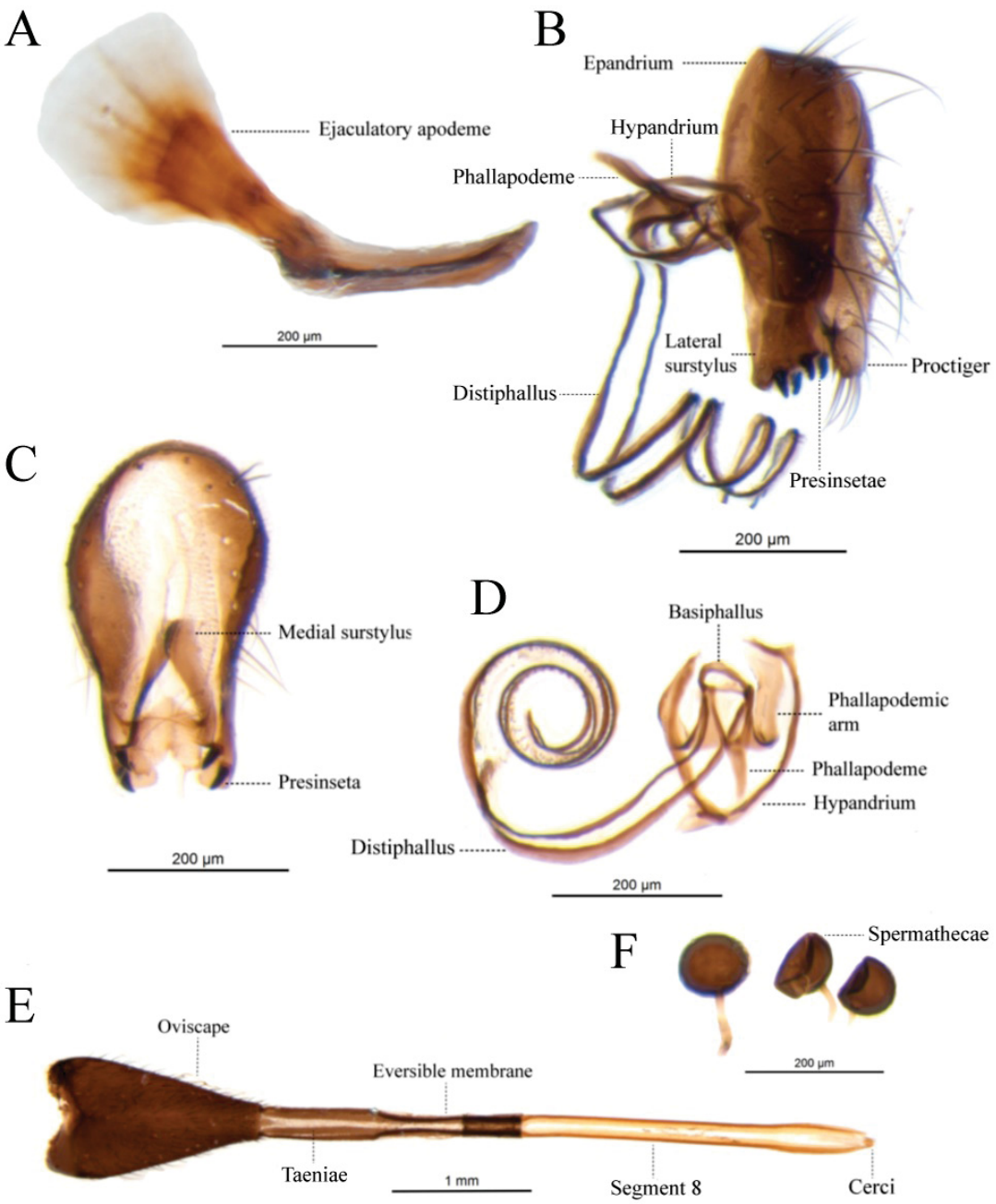


Figure 2. A–D. Male terminalia of *Plagiocephalus*: A. Lateral view of the ejaculatory apodeme (*P. lobularis*); B. Lateral view of the male terminalia (*P. lobularis*) with the epandrium, hypandrium, phallapodeme, distiphallus, lateral surstylus, presinsetae and proctiger indicated; C. Posterior view of the epandrium (*P. latifrons*) with medial surstylus and presinseta indicated; D. Hypandrium, phallapodeme, phallapodemic arm, basiphallus and distiphallus (*P. latifrons*). E–F. Female terminalia of *Plagiocephalus*: E. Dorsal view of the female terminalia (*P. lobularis*) with oviscape, taeniae, eversible membrane, segment 8 and cerci indicated; F. Spermathecae (*P. lobularis*).

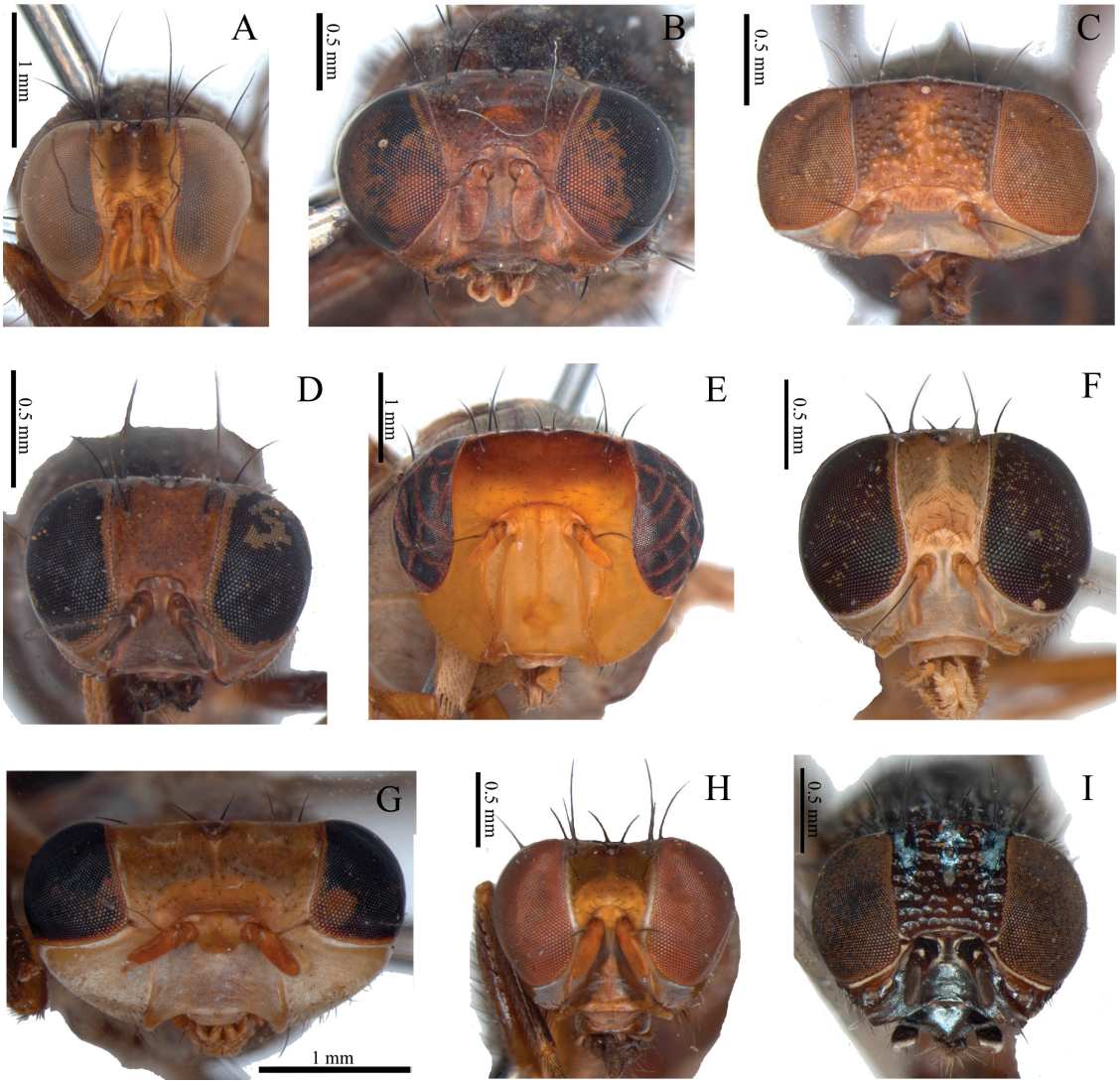


Figure 3. A–I. Head, frontal view: A. *Apterocerina* sp. 1 (male); B. *Bothrometopa determinata* (female); C. *Chondrometopum* sp. (female); D. *Cymatosus polymorphomyioides* (female); E. *Cyrtomostoma gigas* (male); F. *Dasymetopa stigma* (male); G. *Paragorgopis* sp. (male); H. *Pterocerina* sp. 4 (female); I. *Notogramma cimiciforme* (female).

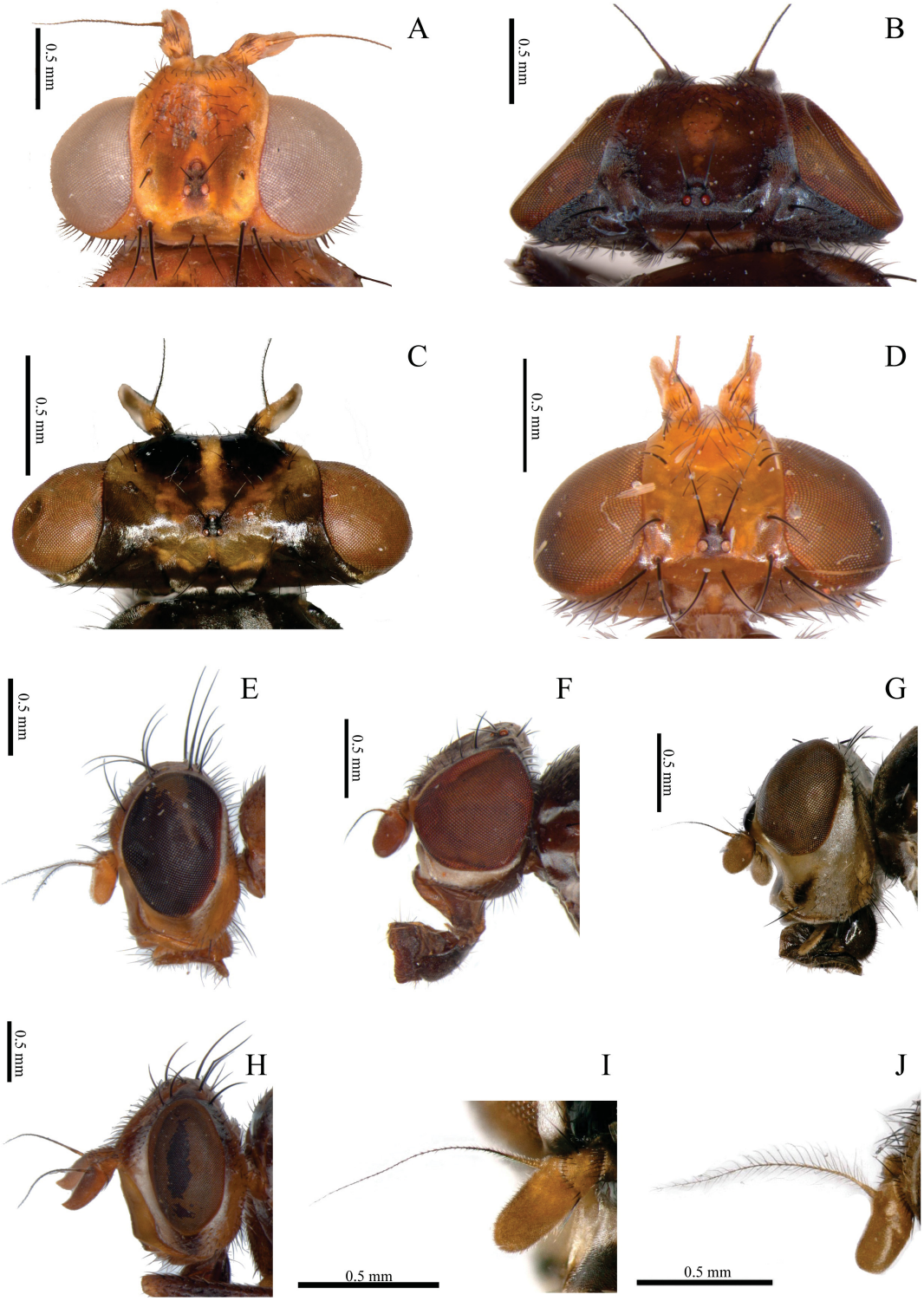


Figure 4. A–D. Head, dorsal view: A. *Apterocerina* sp. 2 (female); B. *Bothrometopa determinata* (female); C. *Plagiocephalus latifrons* (female); D. *Pterocerina nigripes* (female). E–H. Head, lateral view: E. *Aciuroides insecta* (male); F. *Megalaemyia punctulata* (female); G. *Plagiocephalus latifrons* (female); H. *Pterotaenia fasciata* (female). I–J. Antenna, lateral view: I. *Plagiocephalus latifrons* (female); J. *Pterocerina* sp. 2 (female).

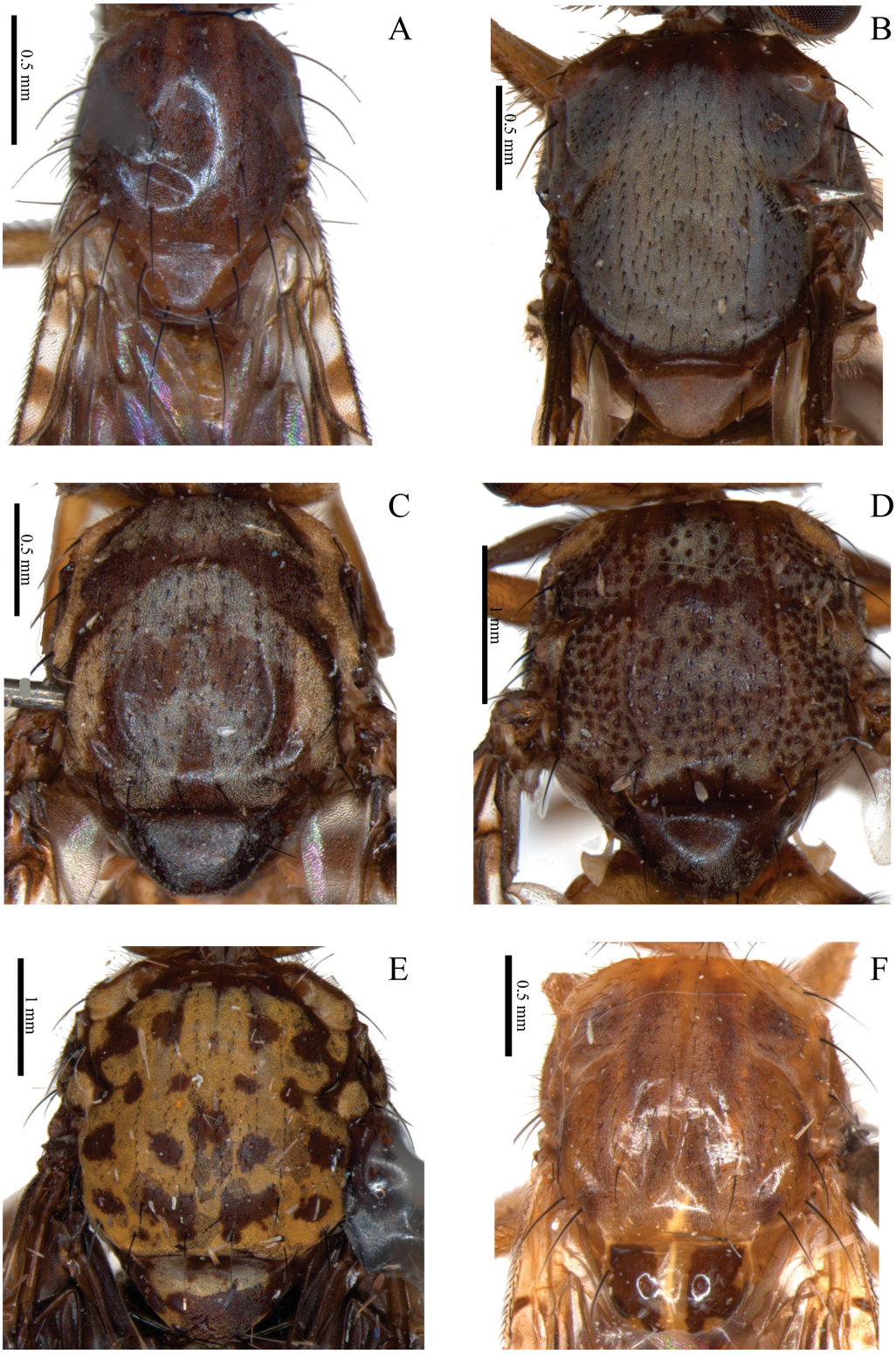


Figure 5. A–F. Thorax, dorsal view: A. *Aciuroides insecta* (female); B. *Dasymetopa stigma* (male); C. *Neomyennis zebra* (male); D. *Paragorgopis* sp. (male); E. *Pterocalla plumitarsis* (female); F. *Xanthacrona bipustulata* (female).

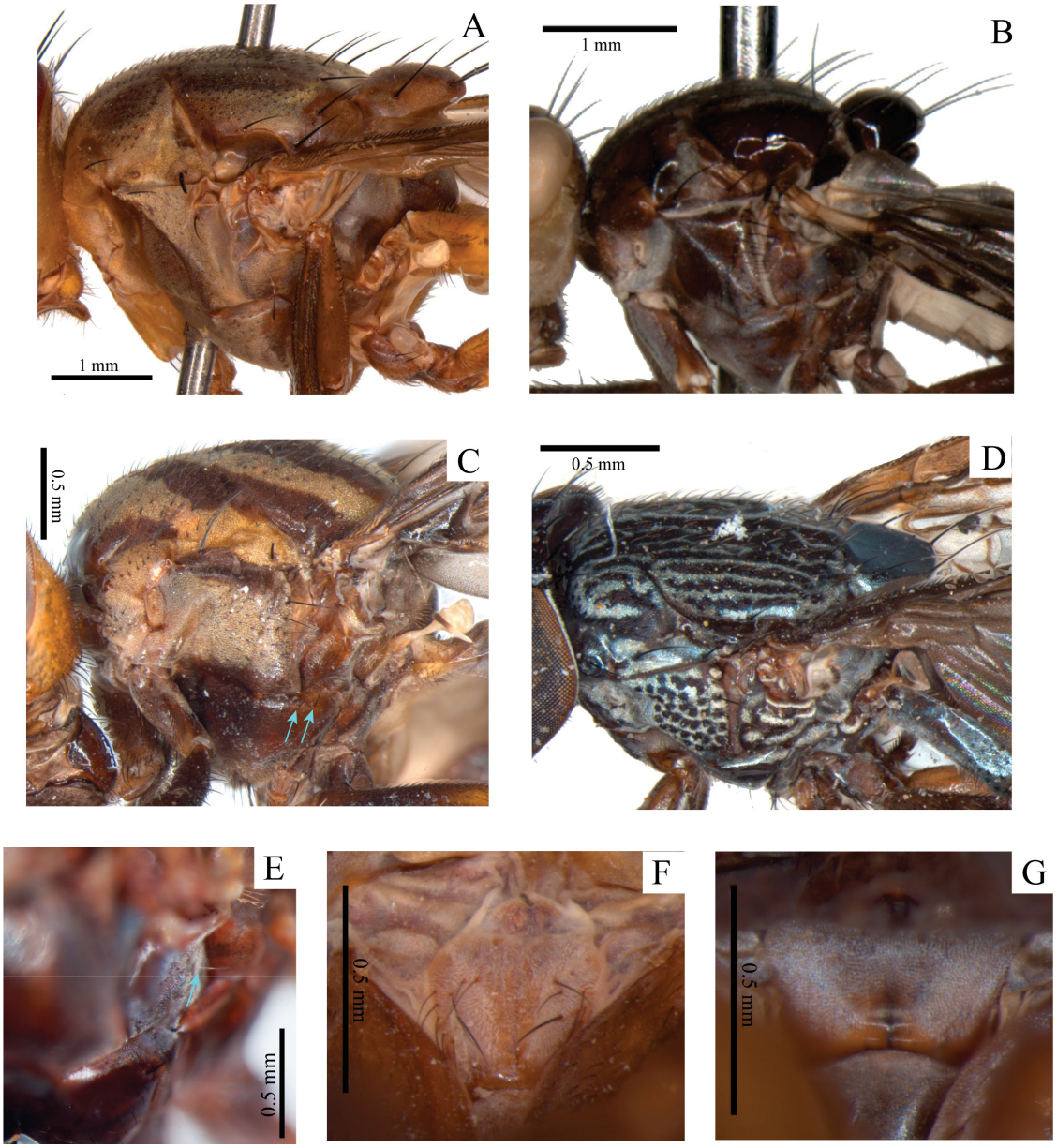


Figure 6. A–D. Thorax, lateral view: A. *Cyrtomostoma gigas* (female); B. *Plagiocephalus latifrons* (female); C. *Neomyennis zebra* (female), arrows indicate the state (1) of the character 32; D. *Notogramma cimiciforme* (male). E. Anepimerum, side view: E. *Pterocerina* sp. 2 (female), arrow indicates the state (0) of the character 33. F–G. Presternum, ventral view: F. *Apterocerina* sp. 2 (female); G. *Plagiocephalus lobularis* (female).

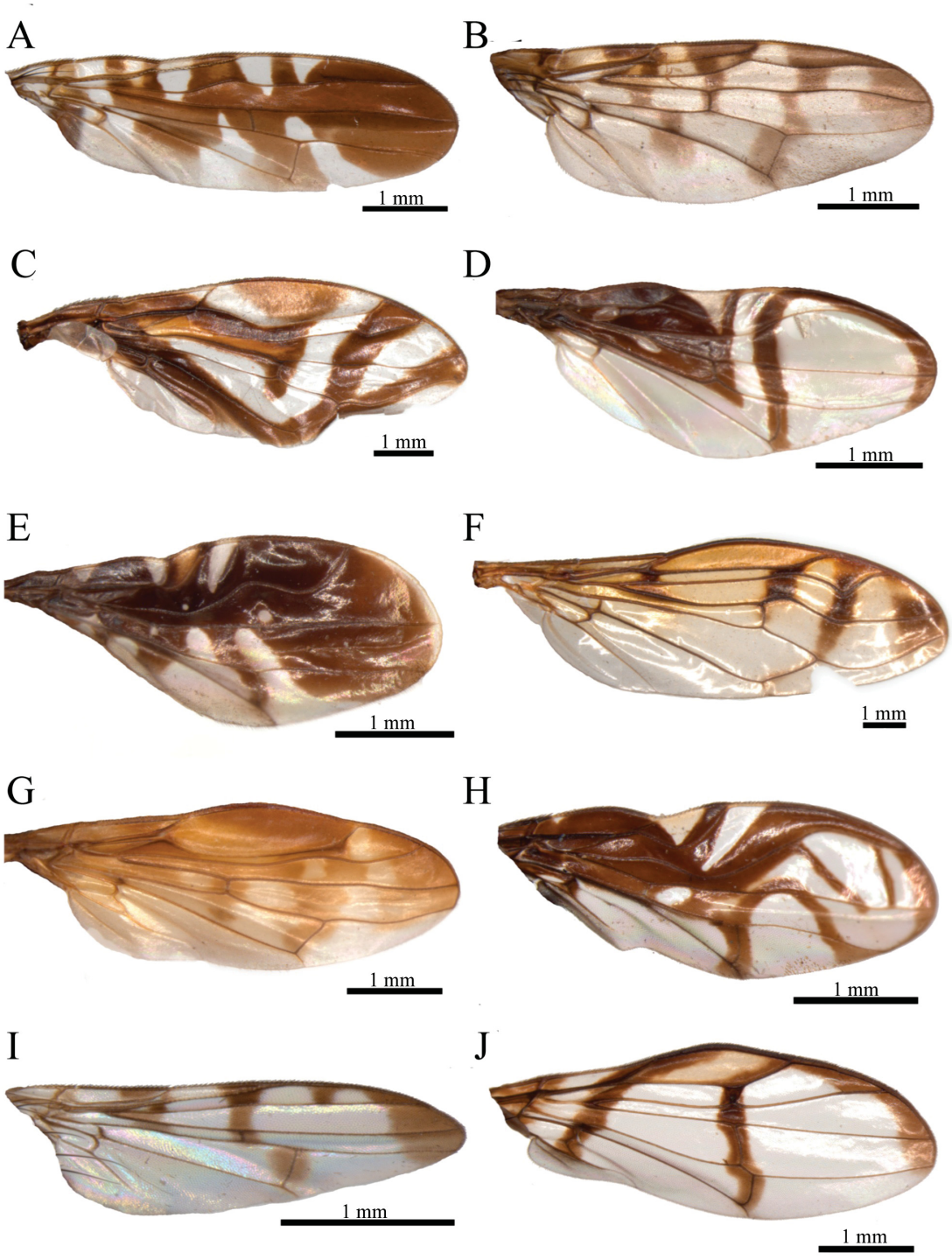


Figure 7 (part I). A–J. Wing, dorsal view: A. *Aciuroides insecta* (female); B. *Apterocerina* sp. 1 (male); C. *Bothrometopa determinata* (male); D. *Chondrometopum* sp. (female); E. *Cymatosus polymorphomyioides* (female); F. *Cyrtomostoma gigas* (male); G. *Dasymetopa nigropunctata* (male); H. *Megalaemyia punctulata* (female); I. *Neoacanthoneura* sp. (female); J. *Neomyennis appendiculata* (male).

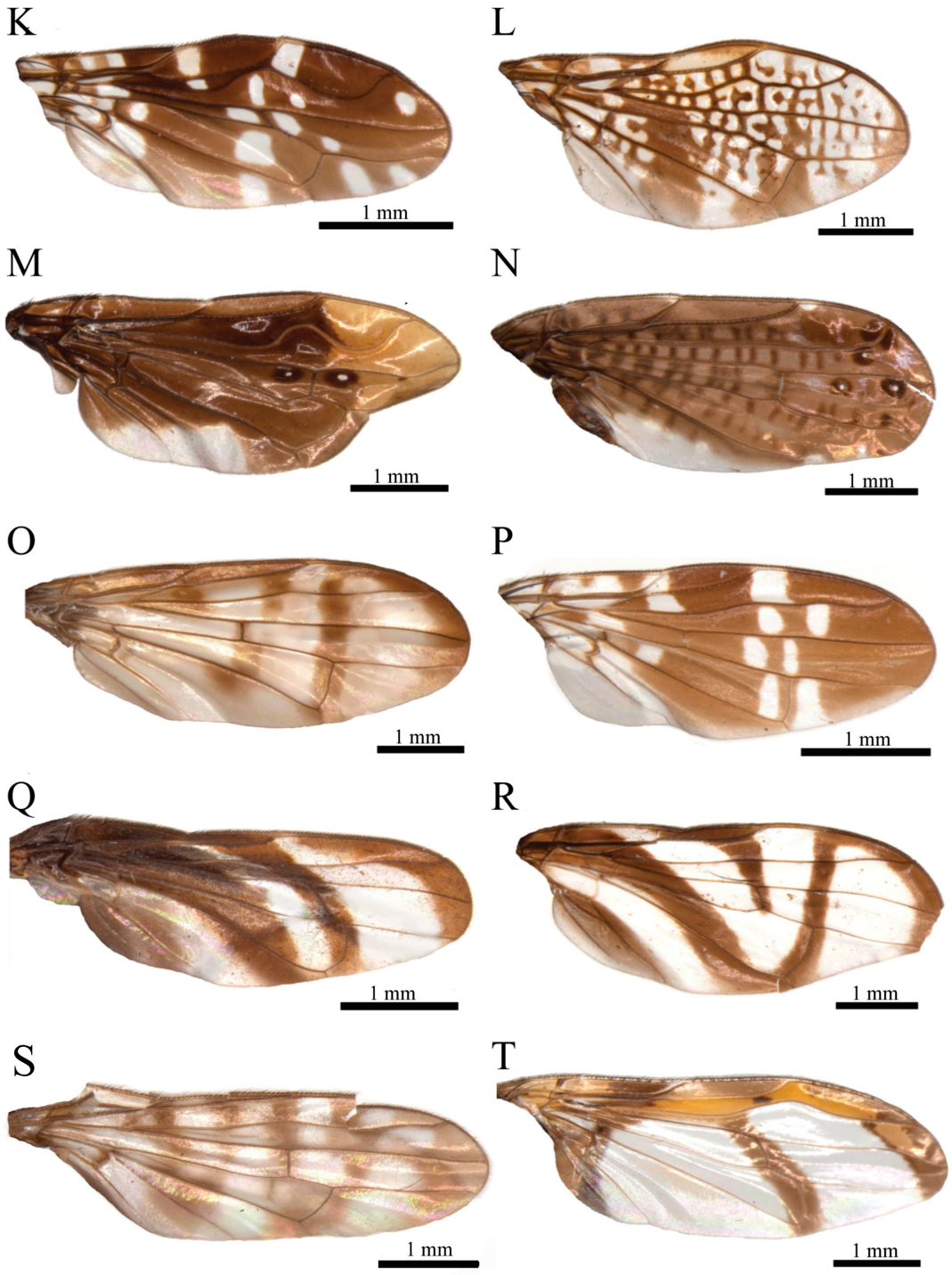


Figure 7 (part II). K–T. Wing, dorsal view: K. *Paragorgopis euryale* (male); L. *Paragorgopis* sp. (male); M. *Pseudopterocalla scutellata* (female); N. *Pterocalla ocellata* (female); O. *Pterocerina* sp. 1 (female); P. *Rhyparella decempunctata* (male); Q. *Terpnomyennis nigra* (female); R. *Terpnomyia augustifrons* (female); S. *Tetrapleura* sp. (female); T. *Xanthacrona bipustulata* (female).

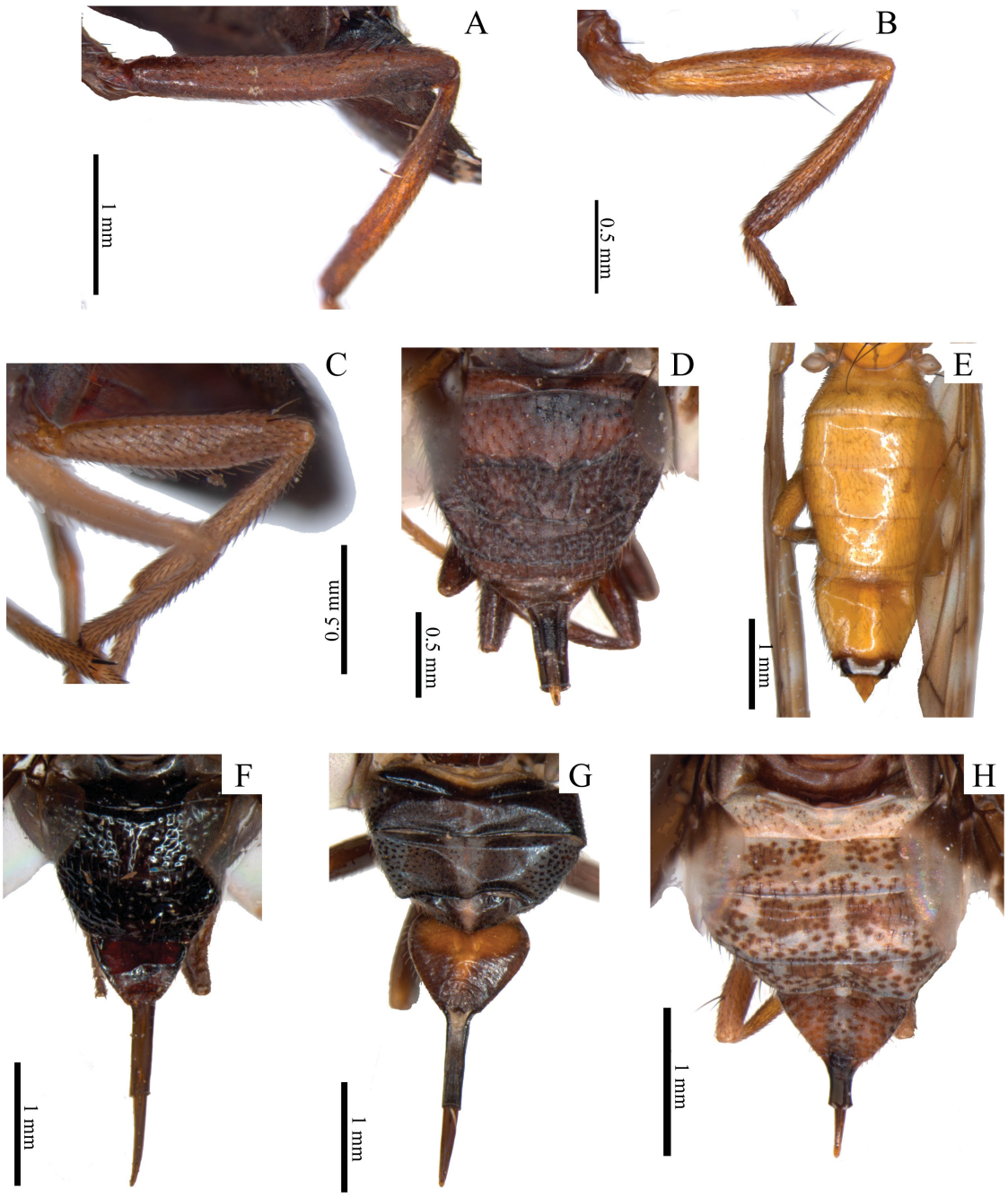


Figure 8. A–C. Hind femur, lateral view: A. *Pterocalla plumitarsis* (female); B. *Pterocerina* sp. 3 (male); C. *Rhyparella decempunctata* (male). D–H. Dorsal view of the abdomen and female terminalia: D. *Cymatosus polymorphomyioides*; E. *Lathrostigma* sp.; F. *Megalemyia punctulata*; G. *Neomyennis zebra*; H. *Pterocalla pantherina*.

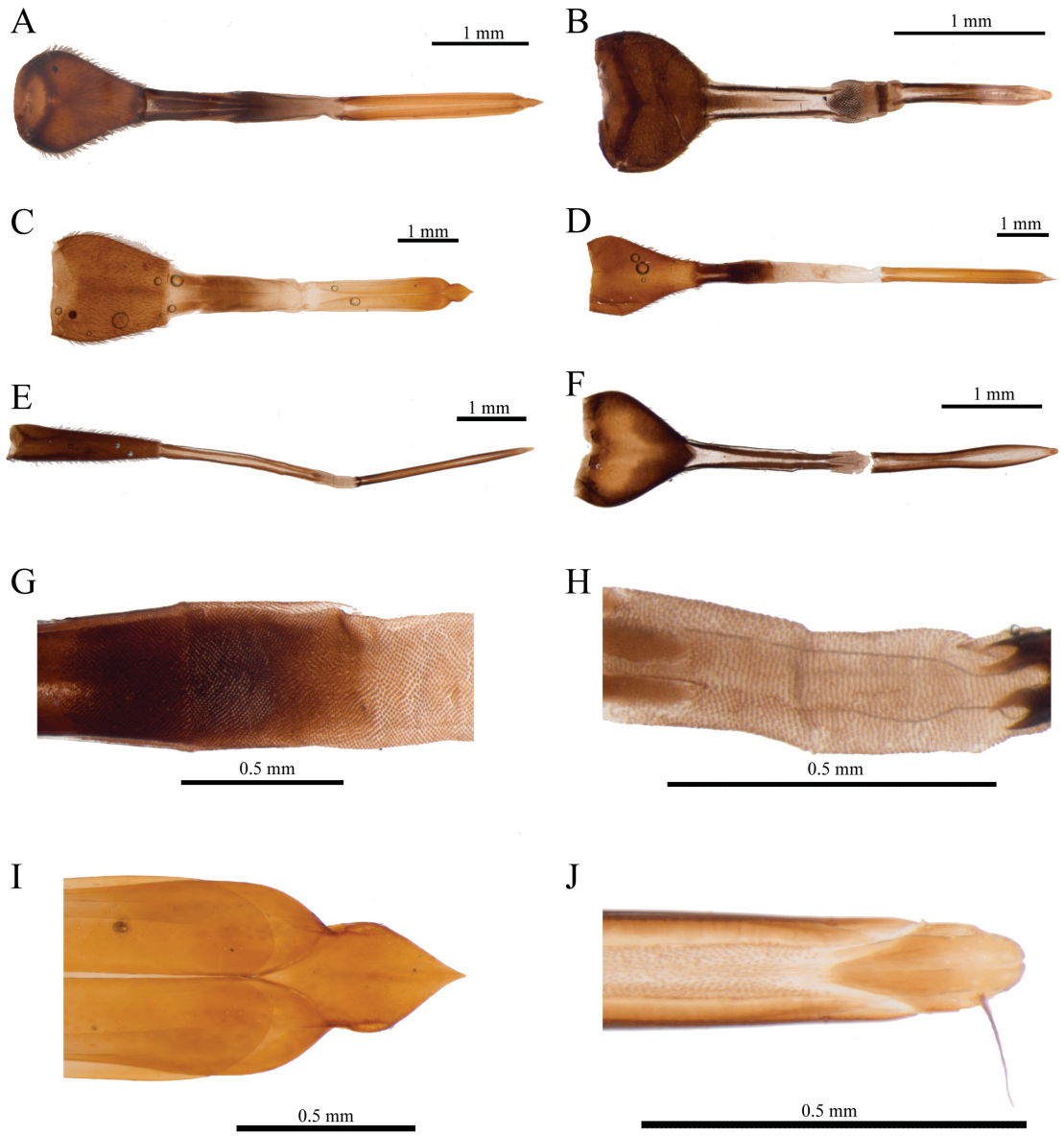


Figure 9. A–H. Oviscape, dorsal view: A. *Apterocerina* sp. 1; B. *Cymatosus polymorphomyioides*; C. *Cyrtomostoma gigas*; D. *Lathrostigma limbatofasciata*; E. *Megalaemyia costalis*; F. *Neomyennis zebra*. G–H. Eversible membrane: G. *Lathrostigma limbatofasciata*; H. *Megalaemyia costalis*. I–J. Cerci, dorsal view: I. *Cyrtomostoma gigas*; J. *Pseudopterocalla scutellata*.

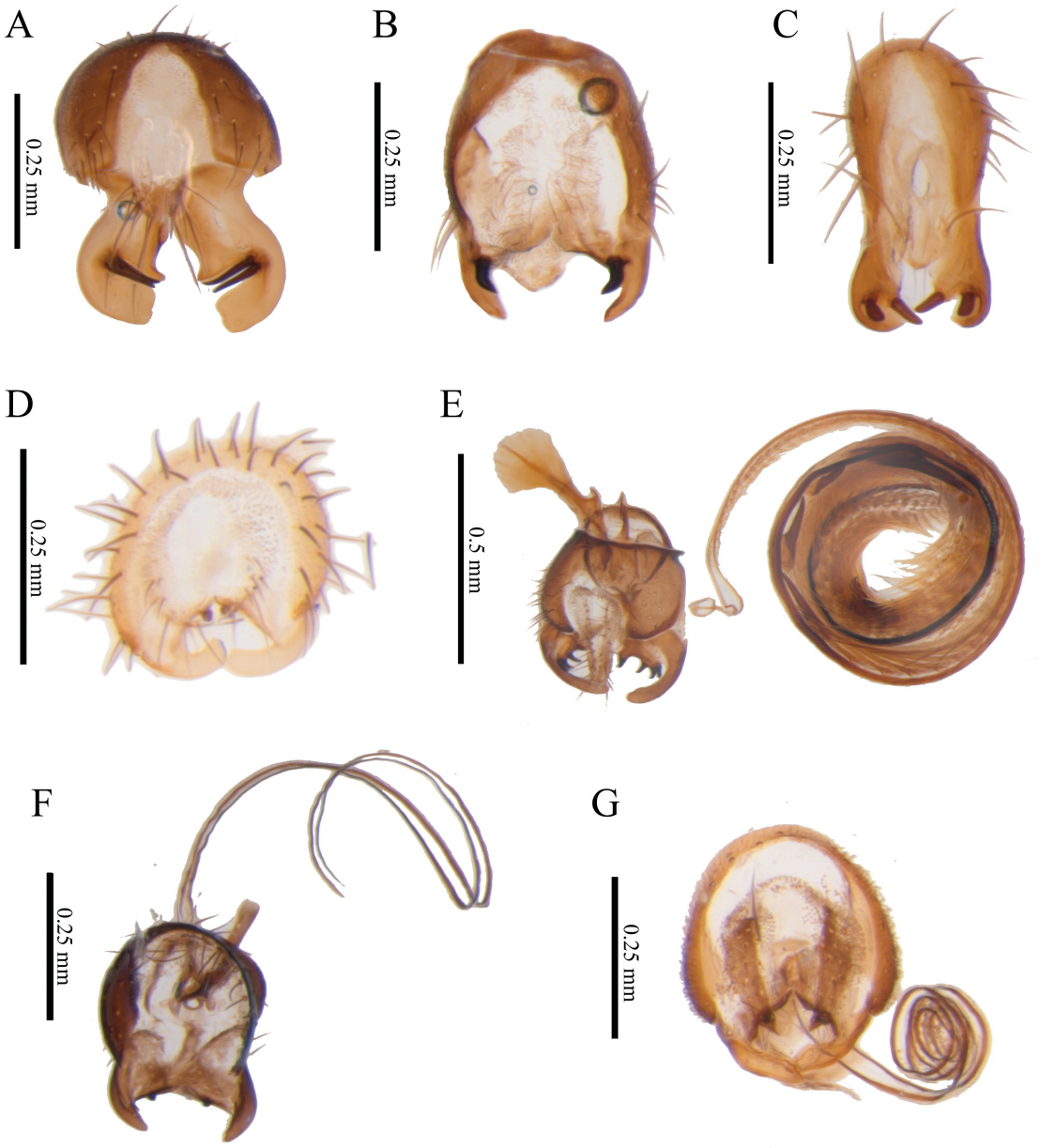


Figure 10. A–D. Epandrium, posterior view: A. *Apterocerina* sp. 2; B. *Pterocalla plumitarsis*; C. *Pterocerina* sp. 3; *Xanthacrona tuberosa*. E–G. Epandrium and distiphallus, posterior view: E. *Acrostictella parallela*; F. *Neomyennis zebra*; G. *Pseudopterocalla obscura*.

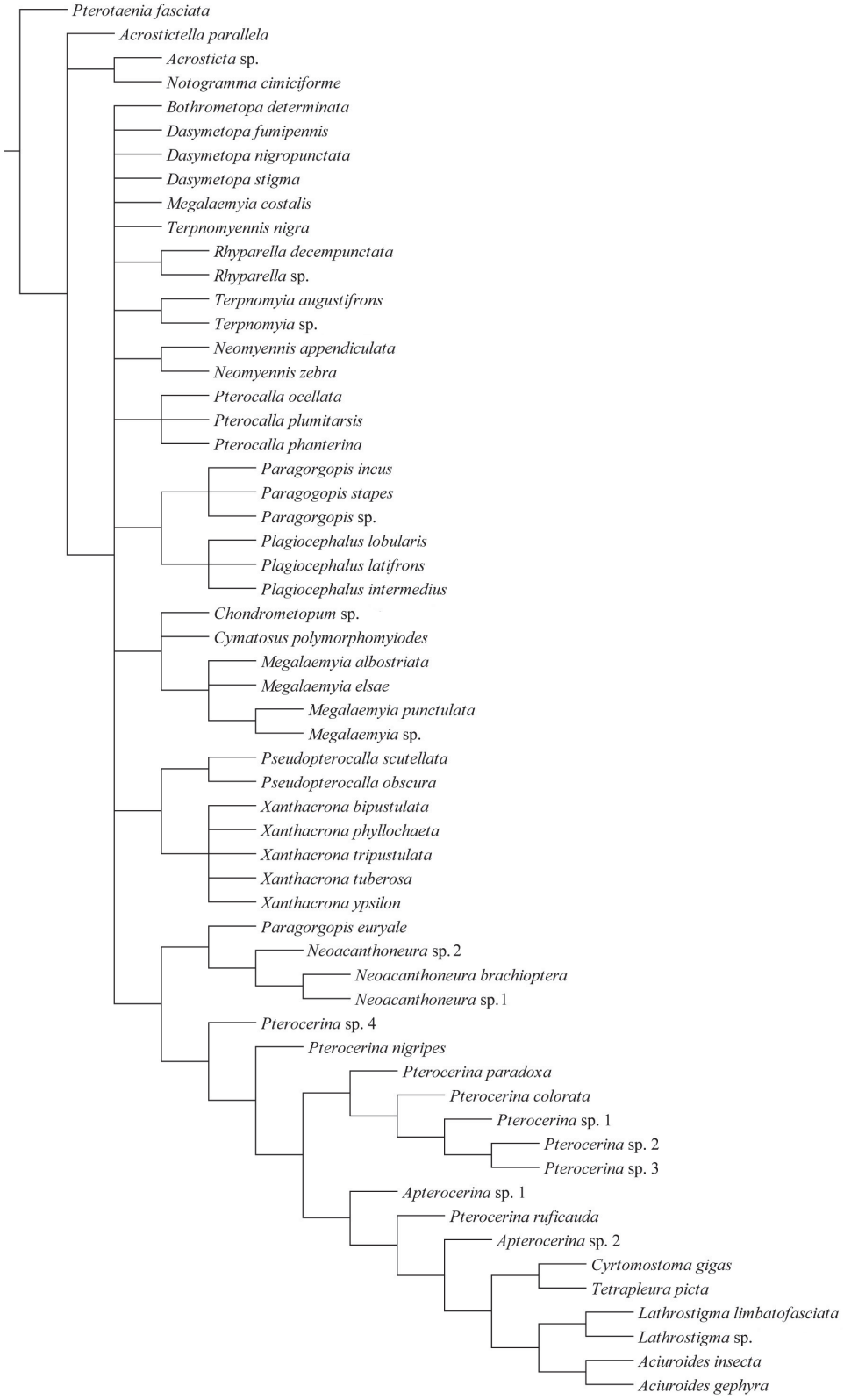


Figure 11. Strict consensus tree generated from a parsimony analysis under equal weighting (L = 565; IC = 25; IR = 61).

Figure 12. Tree generated from a parsimony analysis under implied weighting with $k = 1$ (L = 517; IC = 28; IR = 66).

Figure 13. Tree generated from a parsimony analysis under implied weighting with k = 2–5 (L = 500; IC = 29; IR = 67).

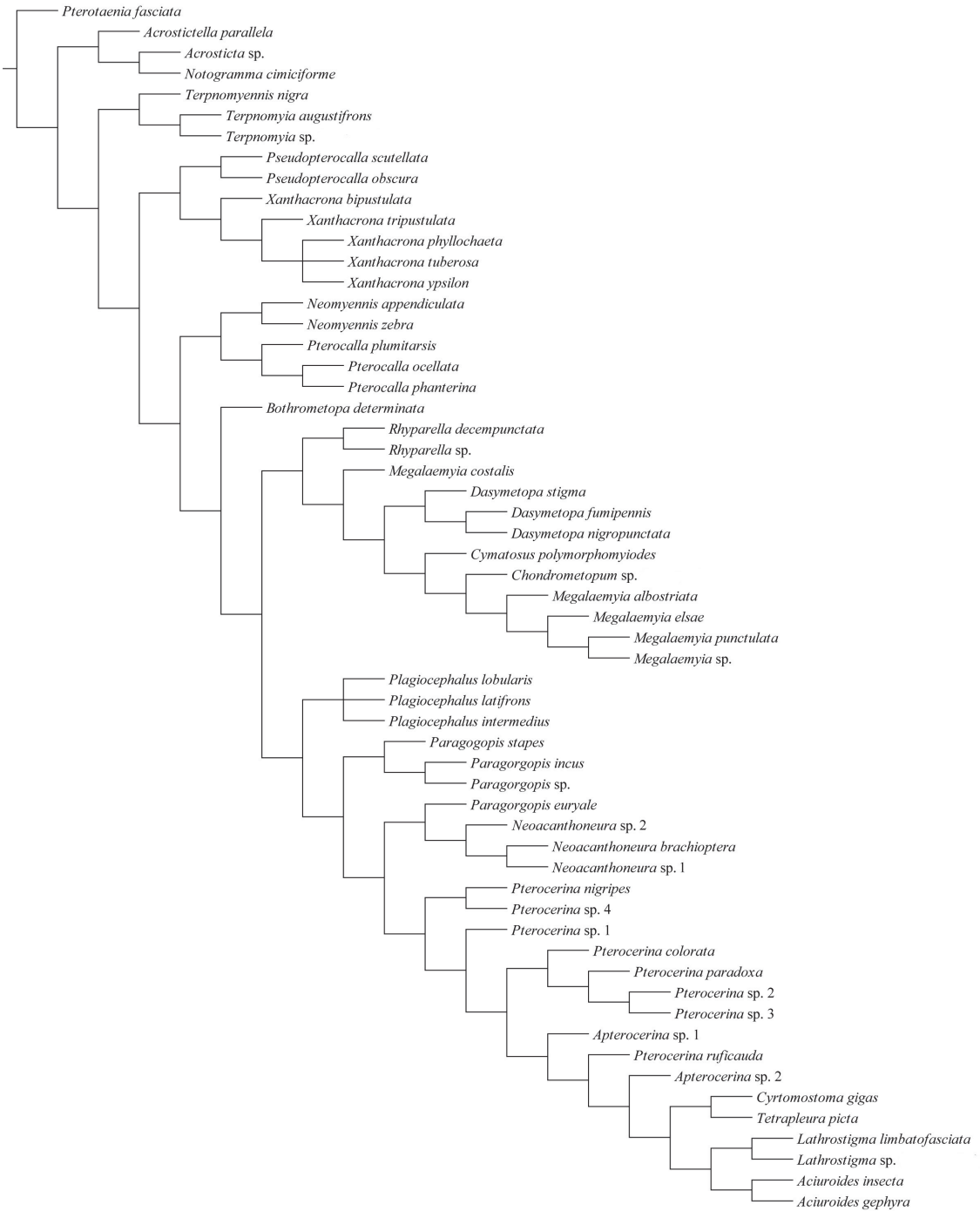


Figure 14. Tree generated from a parsimony analysis under implied weighting with k = 6–9 (L = 495; IC = 29; IR = 68).

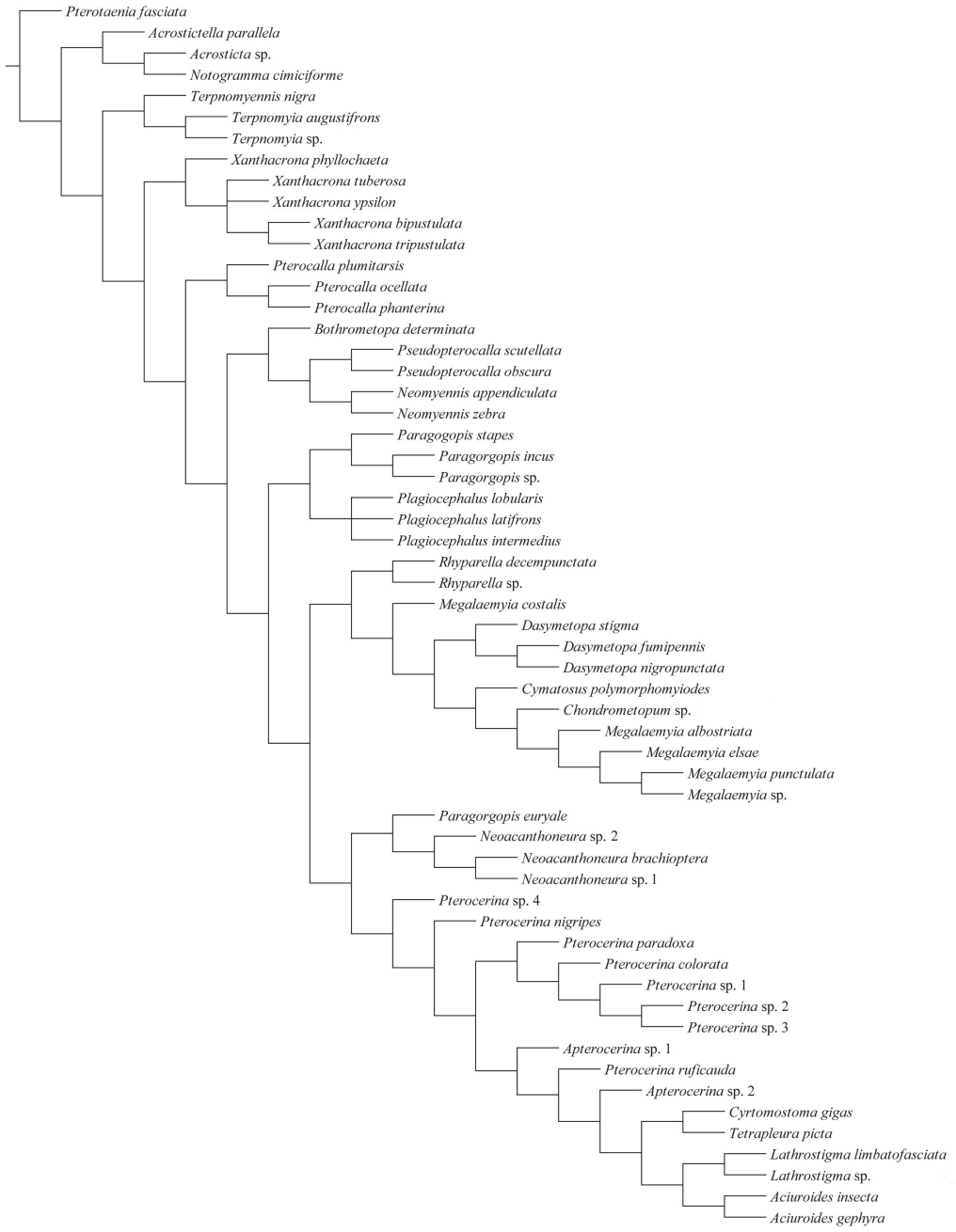


Figure 15. Tree generated from a parsimony analysis under implied weighting with k = 10–13 (L = 492; IC = 29; IR = 68).

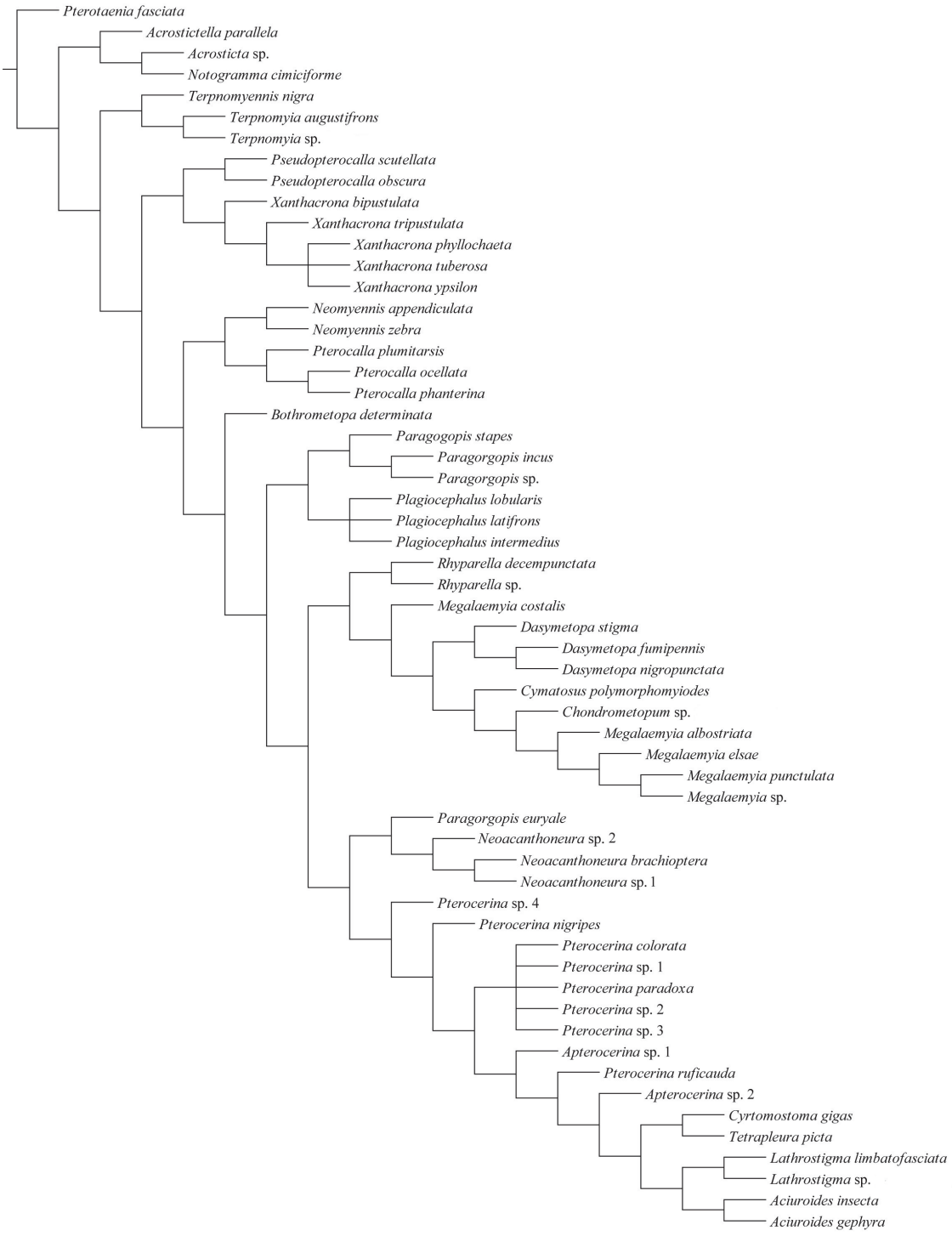


Figure 16. Strict consensus tree generated from a parsimony analysis under implied weighting with k = 14–30 (L = 491; IC = 29; IR = 68).

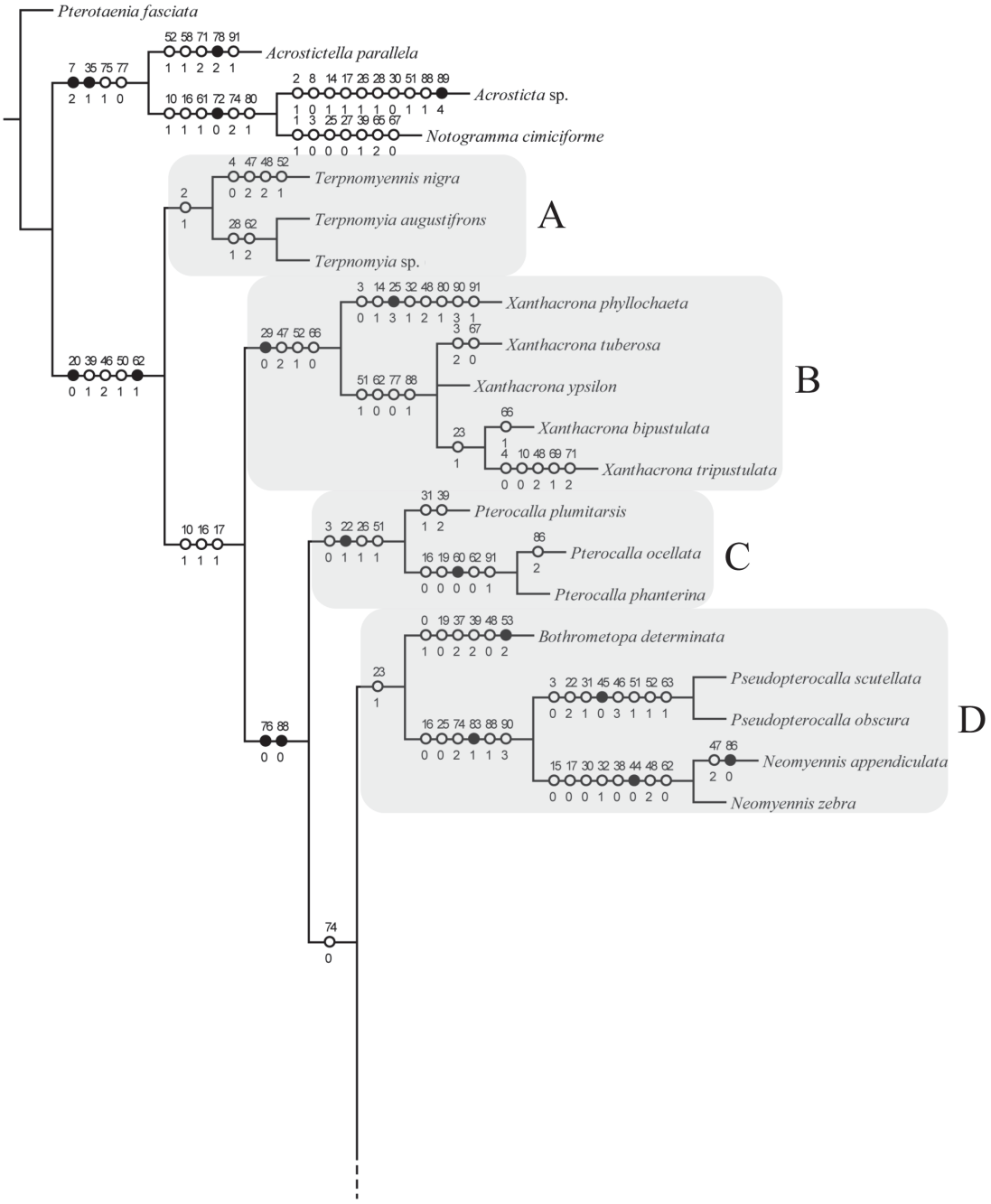


Figure 17 (part I). Tree generated from a parsimony analysis under implied weighting with k = 10–13 showing unambiguous characters supporting each clade. Unique transformations are shown as black circles and homoplastic transformations are shown as white circles.

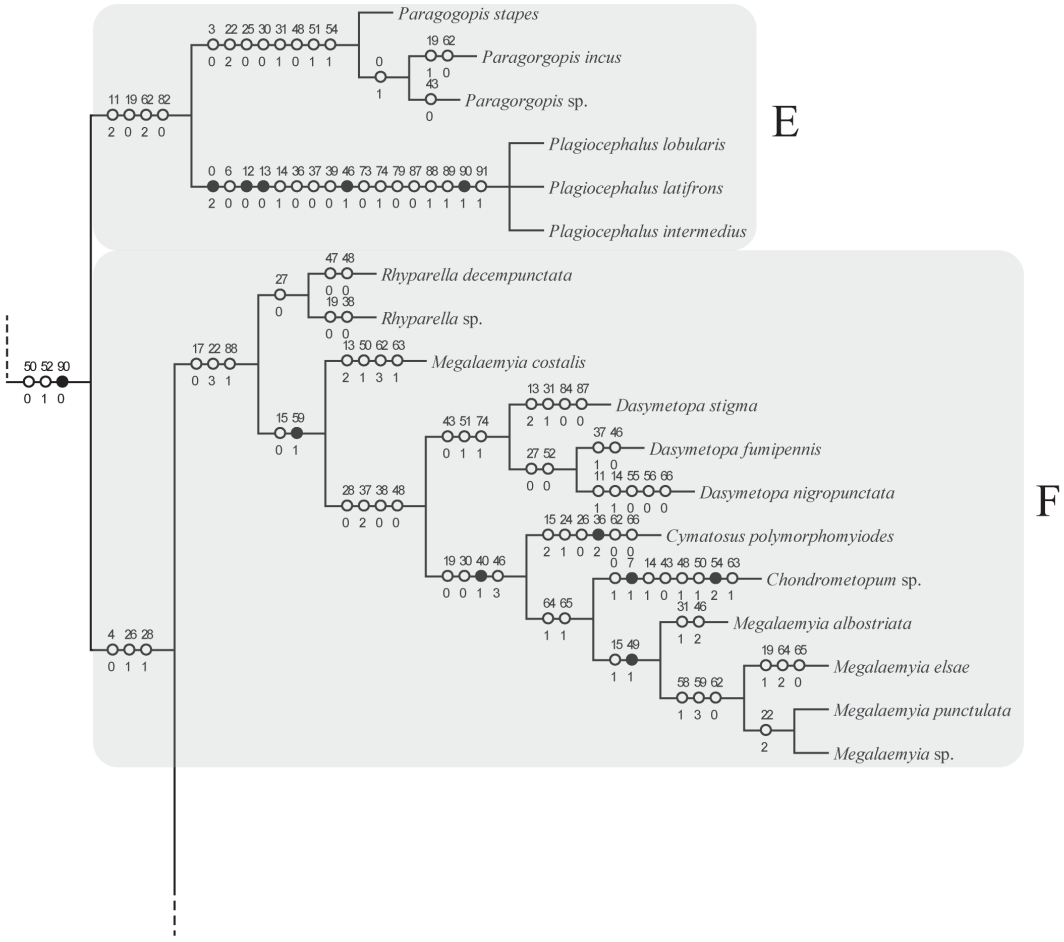


Figure 17 (part II). Tree generated from a parsimony analysis under implied weighting with k = 10–13 showing unambiguous characters supporting each clade. Unique transformations are shown as black circles and homoplastic transformations are shown as white circles.

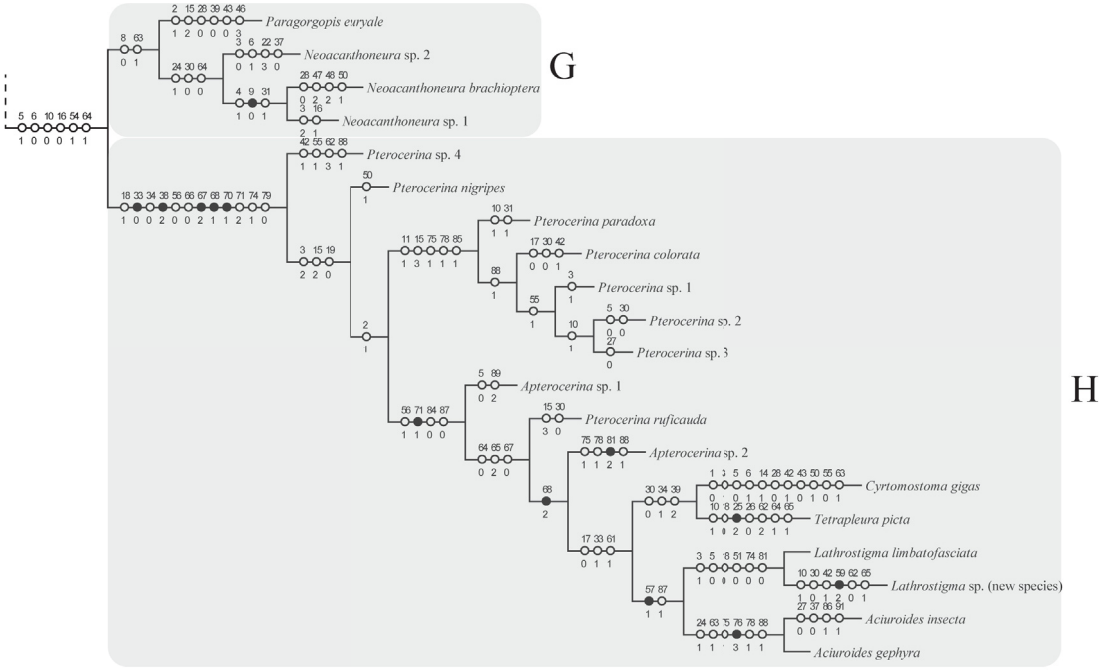


Figure 17 (part III). Tree generated from a parsimony analysis under implied weighting with k = 10–13 showing unambiguous characters supporting each clade. Unique transformations are shown as black circles and homoplastic transformations are shown as white circles.

Figure 18. Phylogenetic reconstruction of Pterocallini generated from a parsimony analysis under implied weighting with k = 10–13 with Relative Bremer Support indicated.

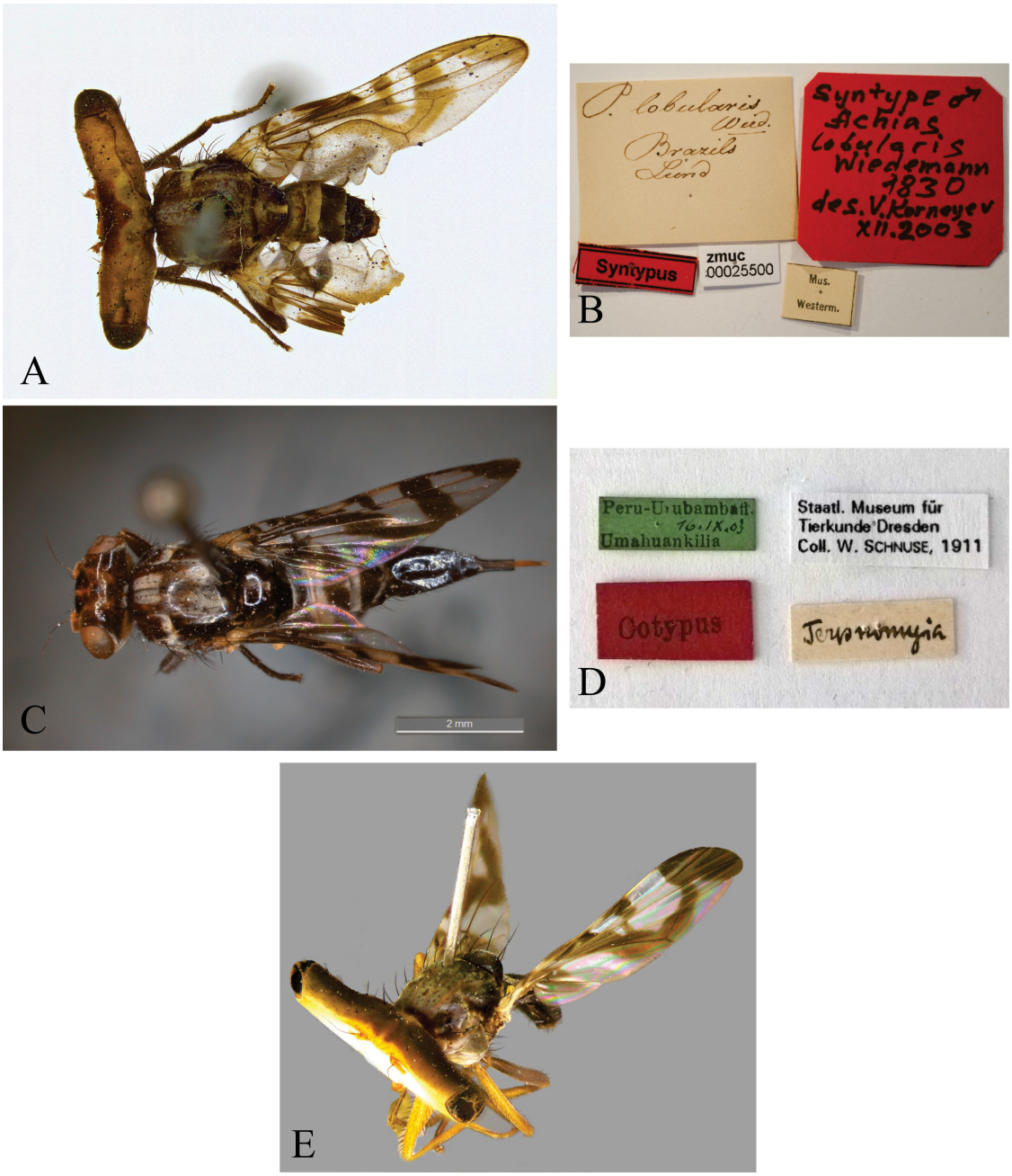


Figure 19. Type material of the species of *Plagiocephalus*: A–B. Lectotype of *Achias lobularis* Wiedemann, 1830a (= *Plagiocephalus lobularis*): A. Habitus; B. Labels. C–D. Syntype of *Terpnomyia latifrons* Hendel, 1909a (= *Plagiocephalus latifrons*): C. Habitus; D. Labels. E–F. Holotype of *Plagiocephalus intermedius* Kameneva, 2004b: E. Habitus; (photograph of the labels not provided).

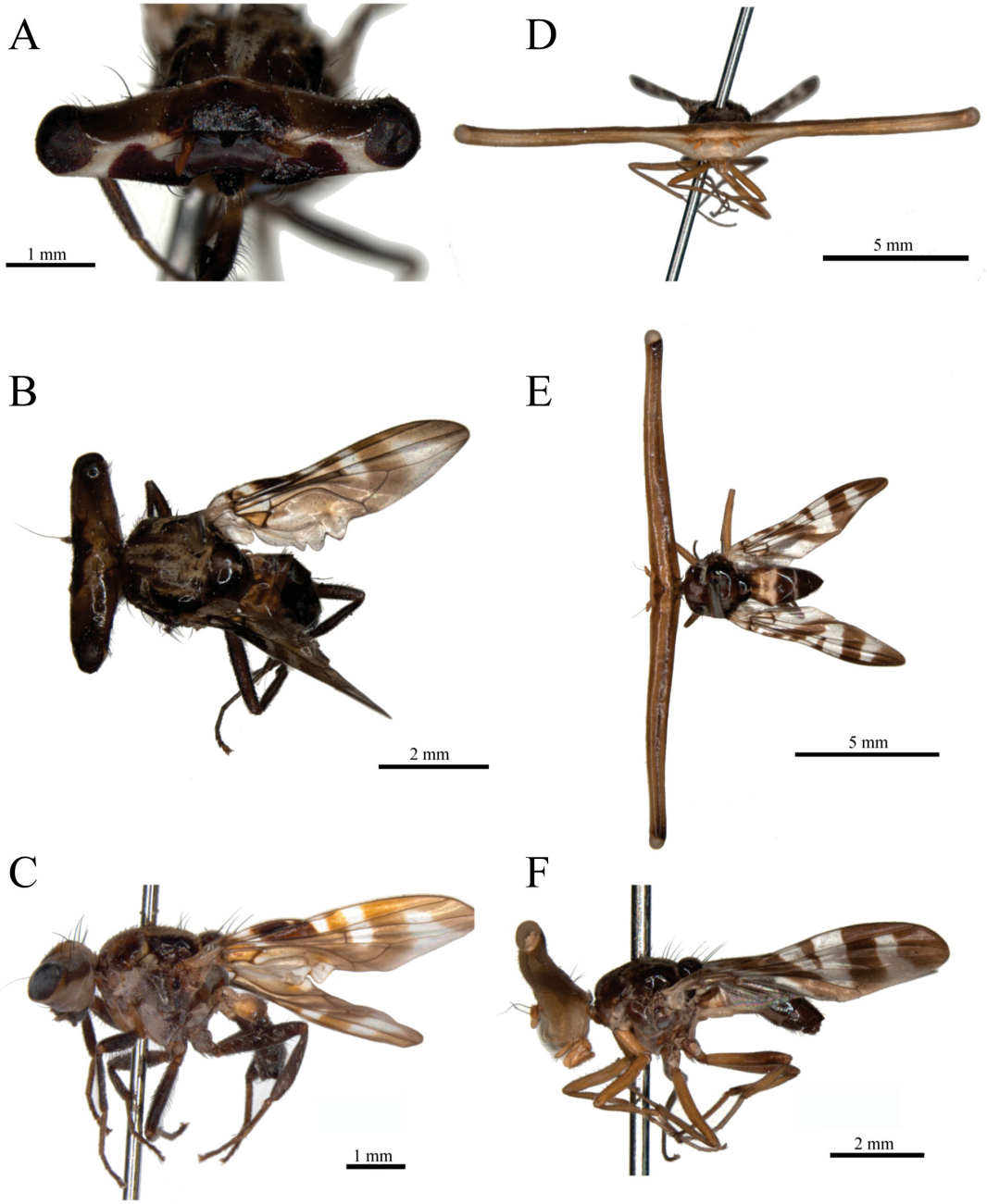


Figure 20. A–C. Male of *Plagiocephalus lobularis*: A. Frontal view of the head; B. Dorsal view of the body; C. Lateral view of the body. D–F. Male of *Plagiocephalus latifrons*: D. Frontal view of the head; E. Dorsal view of the body; F. Lateral view of the body.

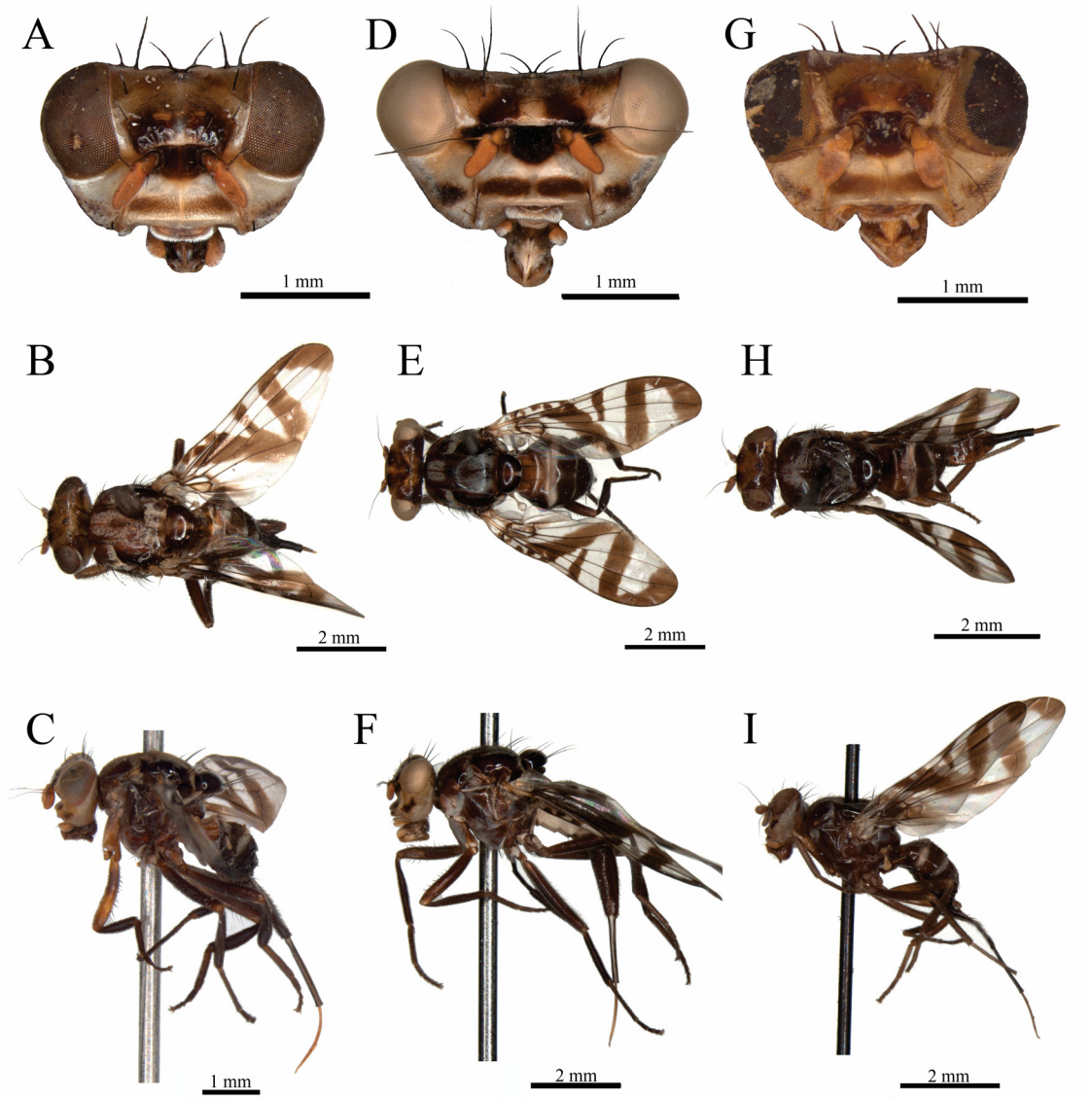


Figure 21. A–C. Female of *Plagiocephalus lobularis*: A. Frontal view of the head; B. Dorsal view of the body; C. Lateral view of the body. D–F. Female of *Plagiocephalus latifrons*: D. Frontal view of the head; E. Dorsal view of the body; F. Lateral view of the body. G–I. Female of *Plagiocephalus intermedius*: G. Frontal view of the head; H. Dorsal view of the body; I. Lateral view of the body.

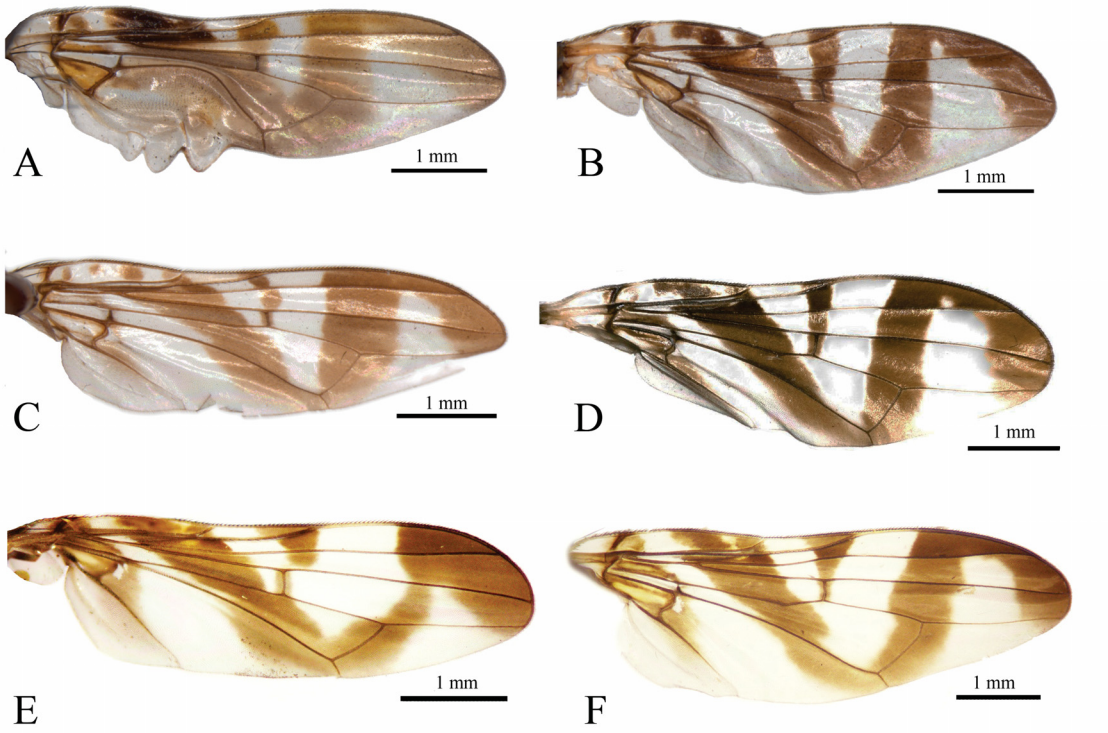


Figure 22. A–B. *Plagiocephalus lobularis*: A. Male wing; B. Female wing. C–D. *Plagiocephalus latifrons*: C. Male wing; D. Female wing. E–F. *Plagiocephalus intermedius*: E. Male wing (photograph of the holotype wing taken by Dr. Valery Korneyev); F. Female wing (photograph of a paratype wing taken by Dr. Valery Korneyev).

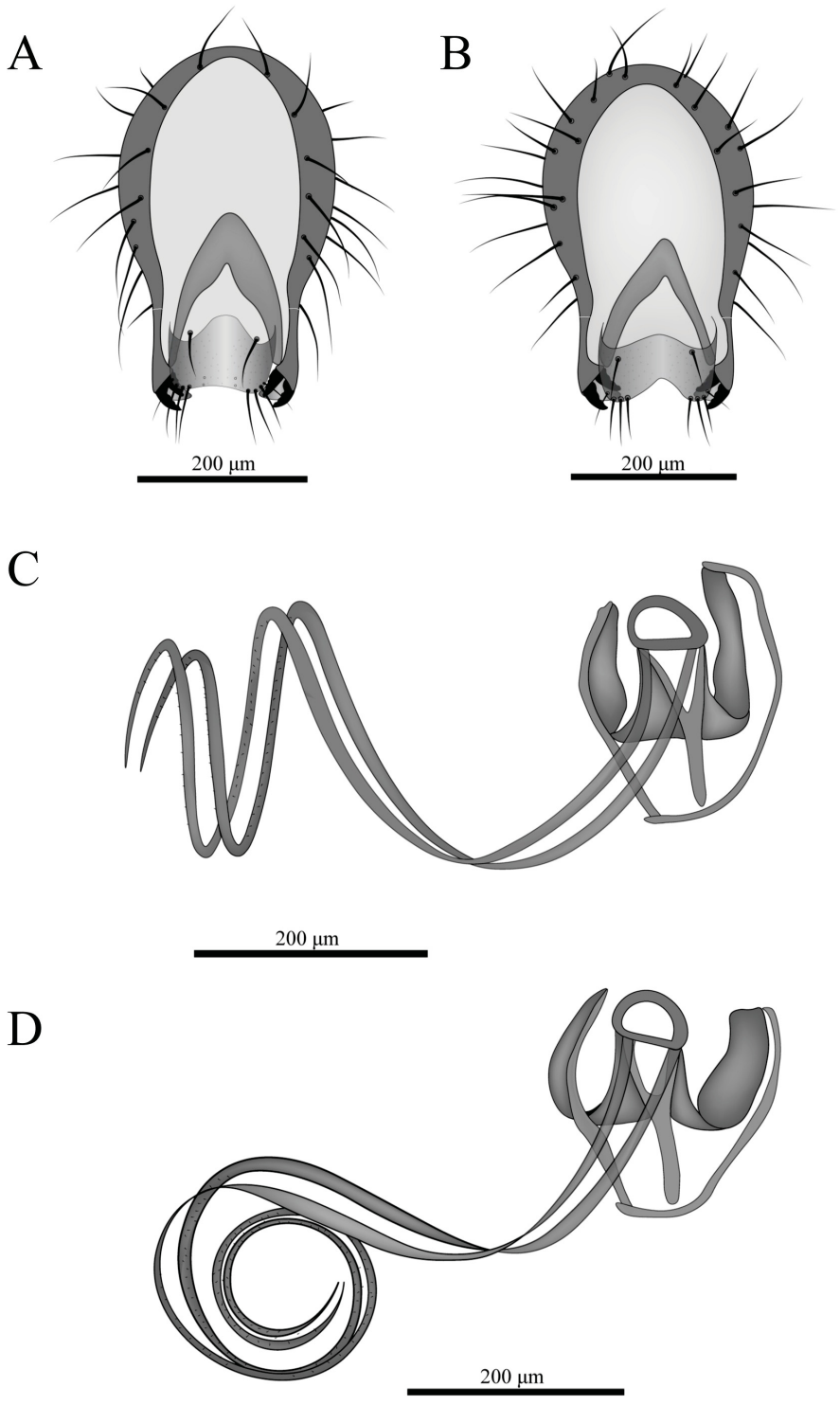


Figure 23. A–D. Male terminalia of *Plagiocephalus*: A. Epandrium of *Plagiocephalus lobularis*; B. Epandrium of *Plagiocephalus latifrons*; C. Hypandrium, basi- and distiphallus of *Plagiocephalus lobularis*; D. Hypandrium, basi- and distiphallus of *Plagiocephalus latifrons*.

Figure 24. Distribution map of *Plagiocephalus*. Red dots: *P. intermedius*; Green circles: *P. latifrons*; Blue circles: *P. lobularis*.

Figure 25. Distribution map of *Plagiocephalus lobularis*. Black circles: localities from the literature; Yellow circles: new records.

Figure 26. Distribution map of *Plagiocephalus latifrons*. Black circles: localities from the literature; Yellow circles: new records.

Figure 27. Distribution map of *Plagiocephalus intermedius*. Black circles: localities from the literature; Yellow circle: new record.

APPENDICES

Appendix 1. Examined material in the phylogenetic analysis

Pterocallini:

Aciuroides Hendel
Type species: *Aciuroides insecta* Hendel, 1914

A. gephyra (Hering, 1918)
Brazil: 1 ♀: Brasilien, Nova Teutonia, xi.1968, Fritz Plaumann *leg*. (MZUSP); 2 ♂ 2 ♀: same data, xi.1970 (MZUSP); 1 ♀: same data, xi.1971 (MZUSP); 1 ♂: Paraná, São José dos Pinhais (Br 277-Km 54), 26.I.1985, C.I.I.F. *leg*. (DZUP).

A. insecta Hendel, 1914
Brazil: 1 ♂ 2 ♀: Brasilien, Nova Teutonia, x.1970, Fritz Plaumann *leg*. (MZUSP); 1 ♀: same data, x.1971 (MZUSP); 1 ♂: Santa Catarina, Nova Teutônia, ii.1967, F. Plaumann *leg*. (MZUSP).

Apterocerina Hendel
Type species: *Apterocerina argentea* Hendel, 1914

Apterocerina sp. 1
Brazil: 1 ♀: Minas Gerais, Sapucai Mirim, Cidade Azul, 7.xi.1953, L. Trav., F. & M. Kuhlmann, C. Gans & S. Medeiros *leg*. (MZUSP); 1 ♀: Paraná, São José dos Pinhais (Br277-Km 54), 16.x.1984, C.I.I.F. *leg*., (DZUP); 1 ♂: same data, 30.1.1985 (DZUP); 1 ♀: same data, 21.v.1985 (DZUP); 1 ♀: same data, 16.vi.1985 (DZUP).

Apterocerina sp. 2
Brazil: 1 ♂: Paraná, São José dos Pinhais (Br277-Km 54), 06.i.1985, C.I.I.F. *leg*. (DZUP); 1 ♀: same data, 22.iii.1985 (DZUP); 2 ♀: São Paulo, Campos do Jordão, 04.i.1970, H. Ebert *leg*. (MZUSP).

Bothrometopa Hendel, 1909
Type species: *Bothrometopa gamma* Hendel, 1909 (synonym junior of *Bothrometopa determinata* (Walker, 1857))

B. determinata (Walker, 1857)
Brazil: 1 ♀: Amapá, Serra do Navio, 6.x.1957, Lane *leg*. (MZUSP); 1 ♀: same data, 21.x.1957 (MZUSP); 1 ♂: Rondônia, Porto Velho, AHE Jirau, Rio Madeira, 09–

19.ix.2011, T. F. Carrijo *leg*. (MZUSP); 1 ♀: Rondônia, Ouro Preto do Oeste, 29.i.1987, C. Elias *leg*. (DZUP).

Chondrometopum Hendel
Type species: *Chondrometopum arcuatum* Hendel, 1909

Chondrometopum sp. (new species)
Brazil: 1 ♀: Japunyba, Angra, i.1935, E. Dorio & L. Travassos *leg*. (MZUSP).

Cymatosus Enderlein
Type species: *Cymatosus polymorphomyioides* Enderlein, 1912

C. polymorphomyioides Enderlein, 1912
Brazil: 1 ♀: Brasilien, Nova Teutonia, vi.1970, Fritz Plaumann *leg*. (MZUSP); 1 ♀: same data, xii.1970 (MZUSP); 1 ♀: same data, iii.1971 (MZUSP); 1 ♀: same data, iv.1971 (MZUSP).

Cyrtomostoma Hendel
Type species: *Cyrtomostoma gigas* Hendel, 1909

C. gigas Hendel, 1909
Brazil: 1 ♀: Mato Grosso, Cáceres, 09.ii.xi.1984, C. Elias *leg*. (DZUP); 1 ♂: Mato Grosso do Sul, Aquidauana, Reserva Ecológica UEMS, 27.viii–11.ix.2011, Lamas, Nihei & eq. *leg*. (SISBIOTA) (MZUSP).

Dasymetopa Loew
Type species: *Dasymetopa lutulenta* Loew, 1868

D. fumipennis Hendel, 1909
Brazil: 1 ♀: Mato Grosso do Sul, Corumbá, Passo do Lontra (BEP), 06–18.ix.2011, Lamas, Nihei & eq. *leg*. (SISBIOTA) (MZUSP); 1 ♀: same data, 18.ix–03.x.2011 (MZUSP).

D. nigropunctata Hendel, 1909
Brazil: 2 ♂ 2 ♀: São Paulo, Itaporanga, N. B. Antonina, i.1946, Barretto *leg.* (MZUSP).

D. stigma Hendel, 1909
Brazil: 1 ♂: Pará, Belém, Sta. Barbara, 23.vi.1965, H. S. Lopes *leg*. (MZUSP).

Lathrostigma Enderlein

Type species: *Lathrostigma limbatofasciata* Enderlein, 1921

L. limbatofasciata Enderlein, 1921
Brazil: 1 ♂: Paraná, São José dos Pinhais (Br277-Km 54), 21–27.viii.1984, C.I.I.F. *leg*. (DZUP); 1 ♀ 26.xi–10.xii.1984, same data, (DZUP); 1 ♂: same data, 12.xii.1984 (DZUP); 1 ♂ 1 ♀: same data, 22.xii.1984 (DZUP); 1 ♀: same data, 23.xii.1984 (DZUP); 1 ♀: same data, 24.xii.1984 (DZUP); 1 ♂: same data, 4.i.1985 (DZUP); 1 ♂: same data, 06.i.1985 (DZUP); 1 ♂: same data, 10–14.i.1985 (DZUP); 1 ♂: same data, 08.iii.1985 (DZUP); 1 ♀: same data, 21.iii.1985 (DZUP); 1 ♂: same data, 22.iii.1985 (DZUP); 1 ♂: same data, 31.iii.1985 (DZUP).

Lathrostigma sp. (new species)
Brazil: 2 ♀: Paraná, São José dos Pinhais (Br277-Km 54), 05–12.xi.1984, C.I.I.F. *leg*. (DZUP); 1 ♂: same data, 03.iii.1985 (DZUP); 1 ♀: same data, 11.iii.1985 (DZUP); 1 ♀: same data, 1–8.x.1985 (DZUP).

Megalaemyia Hendel
Type species: *Megalaemyia elsae* Hendel, 1909

M. albostriata Hendel, 1909
Brazil: 1 ♀: Paraná, Iguassú, xii.1941, Com. E. N. V. *leg*. (MZUSP); 2 ♂: Paraná, Jussara, H. Florestal, 1–3.xi.1974, Exp. Depto. Zoo UFPR (DZUP).

M. costalis Hendel, 1909
Brazil: 1 ♀: Amapá, Rio Felício, 03.viii.?, J. Lane *leg*. (MZUSP); 1 ♀: Amazonas, Manaus, RFA Ducke, 16–20.ix.2010, Cordeiro, D., Grisales, D., Guedes, M. & Haseyama, K. *leg*. (DZUP); 1 ♀: Rondônia, Vilhena, 03.x.1986, C. Elias *leg*. (DZUP); 1 ♀: same data, 04.xii.1986 (DZUP).

M. elsae Hendel, 1909
Brazil: 2 ♀: Acre, Mancio Lima, P. N. Serra do Divisor, 15–17.xi.2015, Feitosa, R. S. M., Ferreira, A. C. & Silva, T. S. R. *leg*. (DZUP).

M. punctulata Hendel, 1909
Brazil: 1 ♀: Paraná, São José dos Pinhais (Br277-Km 54), 31.v.1985, C.I.I.F. *leg*. (DZUP); 1 ♀: Japunyba, Angra, i.1935, E. D. Rad & L. Travassos *leg*. (MZUSP).

Megalaemyia sp. (new species)
Brazil: 1 ♂: Rio de Janeiro, Petrópolis, Taquara, 21.xii.1970, H. S. Lopes *leg*. (MZUSP).

Neoacanthoneura Hendel

Type species: *Neoacanthoneura magnipennis* Hendel, 1914

Neoacanthoneura brachioptera Kameneva, 2012
Brazil: 1 ♀: Paraná, Antonina, Res. N. Guaricica, 25.x.2017, Vasconcelos, A. C. O. *leg*. (DZUP).

Neoacanthoneura sp. 1 (new species)
Brazil: 1 ♀: Brasilien, Nova Teutonia, ix.1971, Fritz Plaumann *leg*. (MZUSP).

Neoacanthoneura sp. 2 (new species)
Brazil: 1 ♀: Rondônia, Porto Velho, Rio Madeira, Área Abunã, AHE Jirau, 17.vi–01.vi.2012, Sanhudo, C. E. D. & Andrioli, F. *leg*. (MZUSP).

Neomyennis Hendel
Type species: *Myennis appendiculata* Hendel, 1909

N. appendiculata (Hendel, 1909)
Brazil: 1 ♀: Espiríto Santo, Itaguaçu, x.1970, P. C. Elias *leg*. (MZUSP); 1 ♀: Paraná, Palmas, Rio Iratim, 16.i.1992, R. Misiuta *leg*. (DZUP); 1 ♂: Rio Grande do Sul, Pelotas, 02.xi.1963, C. M. Biezanko *leg*. (MZUSP); 1 ♀: Santa Catarina, Nova Teutônia, xi.1970, F. Plaumann *leg.* (MZUSP); 1 ♂: São Paulo, Cantareira, Chapadão, xi.1946, Barretto *leg*. (MZUSP); 1 ♂: 226/84 (DZUP).

N. zebra (Hendel, 1909)
Brazil: 1 ♂ 1 ♀: Rio Grande do Sul, Sta. Maria, ix.1963, A. P. Prado *leg*. (MZUSP); 1 ♂ 2 ♀: 226/84 (DZUP).

Paragorgopis Giglio-Tos
Type species: *Paragorgopis maculata* Giglio-Tos, 1893

P. euryale Kameneva, 2004a
Brazil: 1 ♂: Amapá, Serra do Navio, 27.ix.1957, J. Lane leg. (MZUSP); 1 ♀: Amazonas, Curuça, Rio Madeira, 9–10.xi.1975, Exp. Perm. Amaz. (MZUSP); 1 ♀: São Paulo, Araçatuba, Córrego Azul, iii.1947, M. P. Barretto *leg*. (MZUSP).

P. incus Kameneva, 2004a
Peru: 1 ♀: Avispas, SE, Cusco, ix.1962, L. E. Peña *leg*. (MZUSP).

P. stapes Kameneva, 2004a
Ecuador: 1 ♂: W. Zamora (Loja), xi. 1970, L. E. Peña *leg*. (MZUSP).

Paragorgopis sp.
Brazil: 1 ♀: Goyaz (Goiás), Campinas, Borgmeier ET, xii.1925, S. Lopes *leg*. (MZUSP); 1 ♂ 1 ♀: Mato Grosso, Bodoquena, xi.1941, Com. I. O. C. *leg*. (MZUSP); 1 ♀: Mato Grosso, Salobra, i.1941, Com. I. O. C. *leg*. (MZUSP); Mato Grosso do Sul, Miranda, Faz. Guaicurus, vii.2001, Koller, W. W., Araújo, C. P. *leg*. (DZUP).

Plagiocephalus Wiedemann
Type species: *Achias lobularis* Wiedemann, 1830

The material of *Plagiocephalus* used in the phylogenetic analysis is listed in the taxonomical revision (page 43).

Pseudopterocalla Hendel
Type species: *Trypeta obscura* Wiedemann, 1830

P. obscura (Wiedemann, 1830)
Brazil: 1 ♀: Amazonas, Manaus, Res. ZF2, 23–26.ix.2010, Cordeiro, D., Grisales, D., Guedes, M. & Haseyama, K. (DZUP); 1 ♀: Rondônia, Vilhena, 03.x.1986, C. Elias *leg*. (DZUP); 1 ♀: same data, 22.x.1986 (DZUP); 1 ♀: same data, 04.xi.1986 (DZUP); 1 ♂: same data, 19.xi.1986 (DZUP).

P. scutellata (Schiner, 1868)
Brazil: 1 ♀: Rondônia, Porto Velho, AHE Jirau, Rio Madeira, 09–19.ix.2011, T. F. Corrijo *leg*. (MZUSP).
Peru: 1 ♀: Avispas, Cuzco, 20.ix.1962, Luis E. Pena *leg*. (DZUP).

Pterocalla Rondani
Type species: *Dictya ocellata* Fabricius, 1805

P. ocellata (Fabricius, 1805)
Brazil: 1 ♀: Rondônia, Ouro Preto do Oeste, 19.viii.1987, C. Elias *leg*. (DZUP); 1 ♀: same data, 02.xi.1987 (DZUP); 1 ♂: Brasilien, Nova Teutonia, 4.x.1970, Fritz Plaumann *leg*. (MZUSP).

P. plumitarsis Hendel, 1909
Brazil: 1 ♂: Rondônia, Flona Jamari, 3–5.ix.2012, R. R. Cavichioli *leg*. (DZUP); 1 ♀: Rondônia, Vilhena, 12.xi.1986, C. Elias *leg*. (DZUP); 2 ♀: same data, 27.xi.1986 (DZUP); 1 ♀: same data, 04.xii.1986 (DZUP); 1 ♀: same data, 11.xii.1986 (DZUP).

P. phanterina (Walker, 1852)

Brazil: 1 ♀: Ceará, Pacatuba, 24.viii.1973, H. S. Lopes *leg*. (MZUSP); 1 ♂: same data, 23.viii.1973 (MZUSP).

Pterocerina Hendel
Type species: *Pterocerina fenestrata* Hendel, 1909

P. colorata Hendel, 1909
Brazil: 1 ♂: Rio de Janeiro, Rio de Janeiro, 5.vi.1985, J. R. Almeida *leg*. (DZUP).

P. nigripes Hendel, 1909
Brazil: 1 ♀: São Paulo, Barueri, 22.vii.19?5, K. Lenko *leg*. (MZUSP); 1 ♀: São Paulo, Campos do Jordão, Faz. Guarda-Serrote, 23.iii.1963, Rabello, T. F., J. Guimarães & A. Barroso *leg*. (MZUSP).

P. paradoxa Hering, 1941
Brazil: 1 ♂: São Paulo, Barueri, 11.viii.1955, K. Lenko *leg*. (MZUSP).

P. ruficauda Hendel, 1914
Brazil: 1 ♀: Santa Catarina, Nova Teutônia, vi.1967, F. Plaumann *leg*. (MZUSP).

Pterocerina sp. 1
Brazil: 1 ♀: Rio de Janeiro, Itatiaia, Faz. Serra, xi.1945, Barretto *leg*. (MZUSP); 2 ♂: Rio de Janeiro, Petrópolis, 1.iii.1969, H. S. Lopes *leg*. (MZUSP).

Pterocerina sp. 2
Brazil: 1 ♀: Mato Grosso, Cáceres, 03.xii.1984, C. Elias *leg*. (DZUP); 1 ♀: same data, 17.xii.1984 (DZUP); 1 ♀: same data, 12.i.1985 (DZUP).

Pterocerina sp. 3
Brazil: 2 ♂: Goiaz (Goiás), Goianesia, ix.1969, H. Ebert *leg*. (MZUSP); 1 ♂: Ceará, Pacatuba, 24.vii.1973, H. C. Lopes *leg*. (MZUSP).

Pterocerina sp. 4
Brazil: 2 ♀: Rio de Janeiro, Itatiaia, viii.1946, Barretto *leg*. (MZUSP); 1 ♀: São Paulo, Eugênio Letévre, 12–13.i.1977, E. Val *leg*. (MZUSP).

Rhyparella Hendel
Type species: *Rhyparella decempunctata* Hendel, 1909

R. decempunctata Hendel, 1909

Brazil: 1 ♂: Rio de Janeiro, Angra dos Reis, 04.viii.1971, H. S. Lopes *leg*. (MZUSP). 1 ♀: Rio de Janeiro, Grajahu, 27.viii.1939, S. Lopes *leg*. (MZUSP); 1 ♂: same data, 24.x.1939 (MZUSP).

Rhyparella sp. (new species)
Brazil: 2 ♀: Rondônia, Vilhena, 29.x.1986, C. Elias *leg*. (DZUP).

Terpnomyennis Kameneva
Type species: *Myennis nigra* Hendel, 1909

T. nigra (Hendel, 1909)
Brazil: 1 ♀: Amazonas, Retirão do Equador, R. Javari, x.1979, Alvarenga *leg*. (MZUSP).

Terpnomyia Hendel
Type species: *Terpnomyia augustifrons* Hendel, 1909

T. augustifrons Hendel, 1909
Brazil: 1 ♀: Amazonas, Retirão do Equador, R. Javari, x.1979, Alvarenga *leg*. (MZUSP); 1 ♀: Rio de Janeiro, Repr. Rio Grande, Jacarepaguá, xii.1967, M. Alvarenga *leg*. (MZUSP); 1 ♀: Rondônia, Vilhena, 27.xi.1986, C. Elias *leg*. (DZUP).

Terpnomyia sp. (new species)
Ecuador: 2 ♀: Napo, Yasuni Res. Sta., 19–30.x.1998, W. J. Hanson (LACM) (LACM ENT 350638, LACM ENT 350639).

Tetrapleura Shiner
Type species: *Tetrapleura picta* Shiner, 1868

T. picta Shiner, 1868
Brazil: 1 ♀: Minas Gerais, Sapucai Mirim, Cidade Azul, 7.xi.1953, L. Trav., F. & M. Kuhlmann, C. Gans & S. Medeiros *leg*. (MZUSP).

Xanthacrona Wulp
Type species: *Xanthacrona bipustulata* Wulp, 1899

X. bipustulata Wulp, 1899
Brazil: 1 ♀: Maranhão, Fortaleza dos Nogueira, Fazenda Retiro, 28.xi–4.xii.2010, Mielke & Carneiro *leg*. (DZUP); 1 ♀: Mato Grosso, Cáceres, 21.xi.1984, C. Elias *leg*. (DZUP); 2 ♀: same data, 17.xii.1984 (DZUP); 1 ♀: Mato Grosso do Sul, Miranda,

Fazenda Guaicurus, vii.2001, Koller, W. W. & Araújo, C. P. *leg*. (DZUP); 1 ♂: Paraná, Morretes (IAPAR), 19.ii.1985, C.I.I.F. *leg*. (DZUP).

X. phyllochaeta Hendel, 1909
Brazil: 1 ♀: Mato Grosso do Sul, Fazenda Guaicurus, xii.2001, Koller, W. W. *leg*. (DZUP); 2 ♂: Pará, Barreirinhas, Rio Tapajós, x–xi.1970, Exp. Perm. Amaz. (MZUSP); 1 ♀: Pará, Jacareacanga, x.1959, M. Alvarenga *leg*. (DZUP); 1 ♀: São Paulo, Araçatuba, Córrego Azul, ii.1946, Barretto *leg*. (MZUSP).

X. tripustulata Enderlein, 1921
Brazil: 1 ♀: Mato Grosso do Sul, Fazenda Guaicurus, xii.2001, Koller, W. W. *leg*. (DZUP).

X. tuberosa Cresson, 1908
Brazil: 3 ♂ 1 ♀: Mato Grosso do Sul, Miranda, Fazenda Guaicurus, vii.2001, Koller, W. W. & Araújo, C. P. *leg*. (DZUP).

X. ypsilon Enderlein, 1921
Brazil: 1 ♀: Paraná, Antonina, Res. Guaricica, 23–24.x.2017, Savaris, M. *leg*. (DZUP).

Outgroup

Lipsanini:

Acrosticta Loew
Type species: *Acrosticta scrobiculata* Loew, 1910

Acrosticta sp.
Brazil: 1 ♀: Distrito Federal, Brasilia, Córrego CO, 23.ix.2004 (DZUP); 1 ♂: Mato Grosso, Cáceres, 13.xi.1984, Buzzi, Mielke, Elias, Casagrande *leg*. (DZUP); 2 ♀: Rondônia, Vilhena, 03.x.1986, C. Elias *leg*. (DZUP); 1 ♂: same data, 23.x.1986 (DZUP); 1 ♀: same data, 27.x.1986 (DZUP).

Notogramma Loew
Type species: *Notogramma cimiciforme* Loew, 1868

N. cimiciforme Loew, 1868
Brazil: 2 ♂ 2 ♀: label lacking information, C.I.I.F. *leg*. (DZUP).

Cephallini:

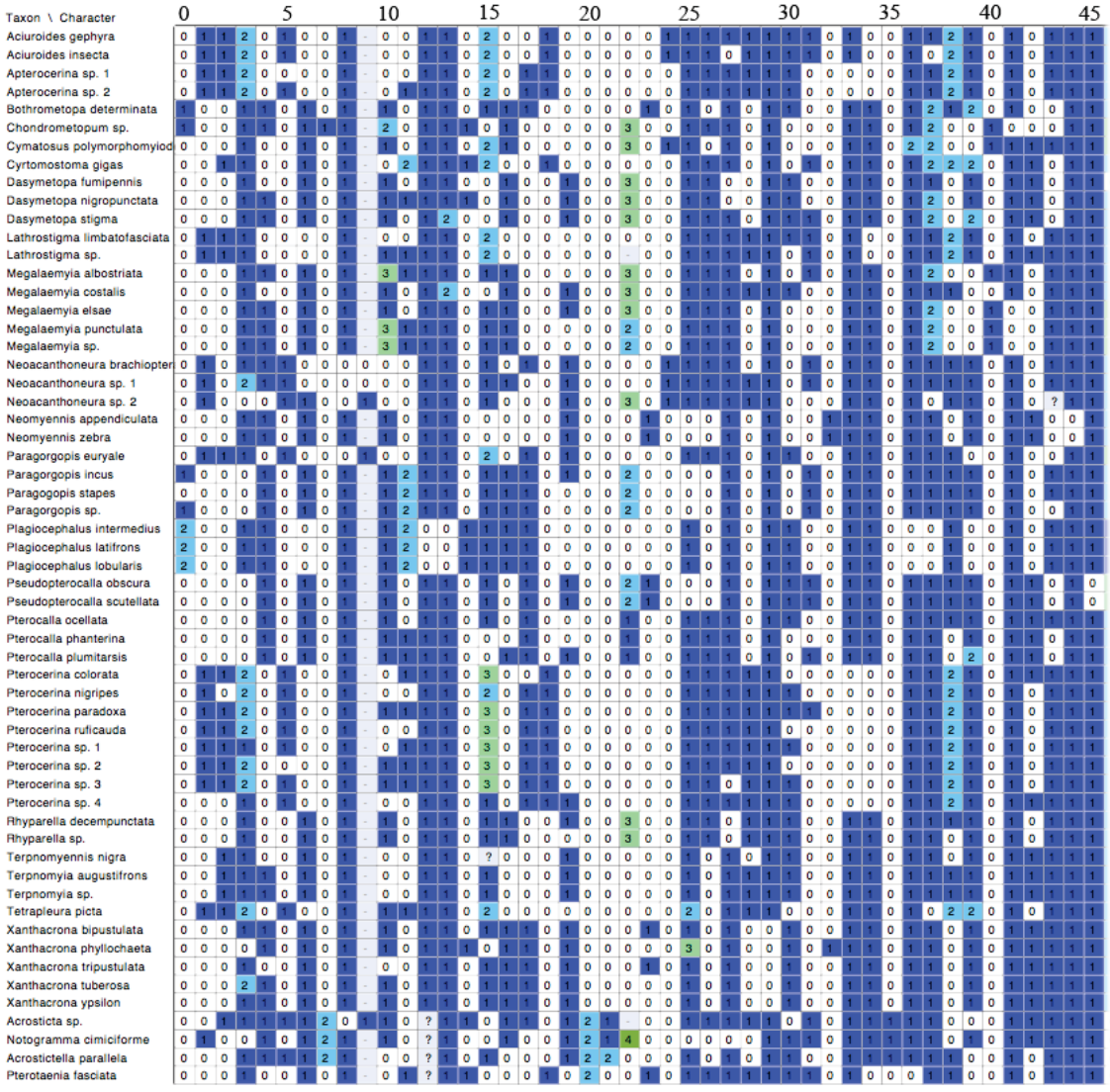
Acrostictella Hendel
Type species: *Acrostictella parallela* Hendel, 1914

A. parallela Hendel, 1914
Brazil: 4 ♂ 1 ♀: Paraná, Pinhão, Salto Segredo, 19.i.1992, R. Misiuta *leg*. (DZUP).

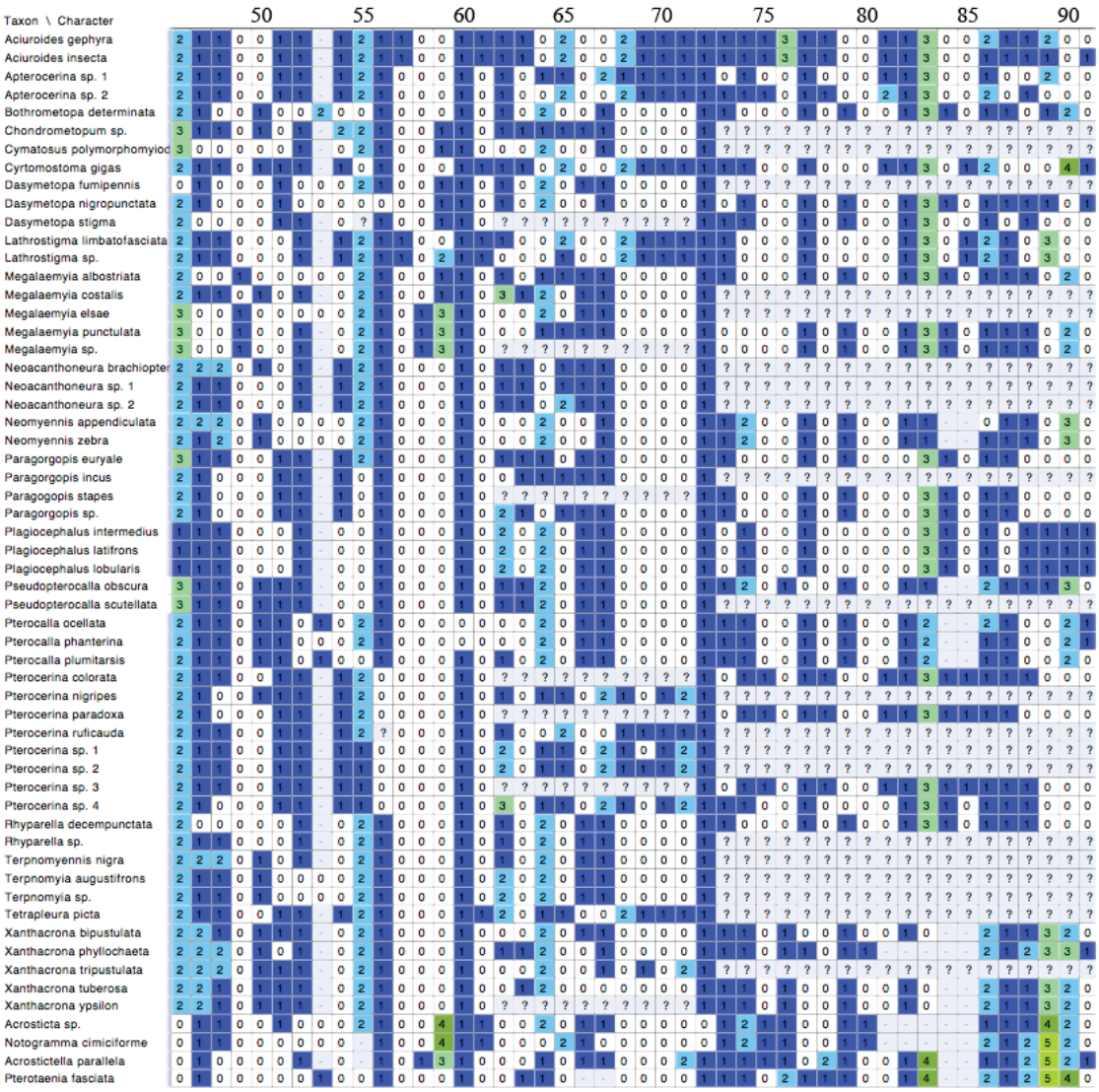
Pterotaenia Rondani
Type species: *Ortalis fasciata* Wiedemann, 1830
(monotypic)

P. fasciata (Wiedemann, 1830)
Brazil: 2 ♂ 3 ♀: Paraná, Curitiba, 24.iii.1975, S. Laroca *leg*. (DZUP).

Appendix 2 (part I). Matrix of morphological characters of Pterocallini



Appendix 2 (part II). Matrix of morphological characters of Pterocallini



Appendix 3. Manuscript: Static allometry in two species of a Neotropical stalk-eyed fly (journal chosen for submission: Journal of Zoology)

Static allometry in two species of a Neotropical stalk-eyed fly

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Abstract

Eyestalk is a sexually selected trait that has evolved multiple times within the true flies (Diptera). After diopsids have inspired a number of studies on sexual selection and allometry of stalked eyes, our study aims to test for covariance of eyestalks and body size in two species of a Neotropical genus of flies. We obtained morphological measurements of eye length and body size from 87 specimens of *Plagiocephalus latifrons* and 61 specimens of *Plagiocephalus lobularis*. We performed a simple regression analysis and calculated the allometric slope of the traits of the species. We found an almost isometric relation of the eyes of females in relation to body size of both species, and an extraordinarily steep and nearly equal positive static allometric relation between the eyestalks and body size of males of *P. latifrons* and *P. lobularis* (b = 3.14 and b = 3.15, respectively). We also found a great difference in the mean of eye length and intercept between these two species. From our results, we could conclude that the allometric slope in *Plagiocephalus* was not influenced by sexual selection on trait size alone and that the intercept is under more variation during evolution than the allometric slope in this group of flies.

Keywords: morphological evolution, scaling relationship, sexual dimorphism, sexual selection, eyestalks.

Introduction

The eyestalks in true flies evolved several and independent times during the evolutionary history of Diptera (Buschbeck *et al.*, 2001). It is known that eight families of true flies (Diopsidae, Drosophilidae, Micropezidae, Periscelididae, Platystomatidae, Richardiidae, Tephritidae and Ulidiidae) exhibit eyestalks, one of the most bizarre morphologies found in animals (Sivinski, 1997; Wilkinson & Dodson, 1997). Sexual selection usually acts with more intensity upon males (Darwin, 1871; Andersson, 1994), which, with exception of some diopsids species, is the only sex that presents stalked eyes (Baker & Wilkinson, 2001). The development of these ornamental traits in males demand viability costs, but, on the other hand, they confer a potential increase in mating success (Buckhardt *et al.*, 1994; Wilkinson & Reillo, 1994; David *et al.*, 2000; Cassidy *et al.*, 2014).

Allometry describes variation in morphology, including sexual ornaments, or other life-history traits in relation to the size of the body (Gould, 1966; Pélabon *et al*., 2014). Allometric relationships can be found across individuals of the same species in the same developmental stage, across different species and across ontogeny. Static Allometry describes the variation in trait size in the same developmental stage of a species, Evolutionary Allometry evaluates the covariation among species between mean trait size and mean body size, while Ontogenetic Allometry assesses changes in traits size through the developmental stages of an organism (Gould, 1966; Cheverud, 1982; Bonduriansky, 2007b; Pélabon *et al*., 2014). When the growth regulation varies differently between a trait and the size of an organism, a positive or negative allometric relation evolves. A positive allometric relation is characterized when the allometric slope of the covariance between a trait and body size is higher than one in the power-law function $Y = aX^b$, where b is the parameter describing the relationship between body and trait size (Gould, 1966; Bonduriansky & Day, 2003; Pélabon *et al.*, 2014).

The evolution of positive allometry has been extensively subject of debate. There is a widespread idea in the literature that secondary sexual traits and directional selection almost universally leads to an expression of positive allometry (*e.g.* Green, 1992; Petrie, 1992; Kodric-Brown *et al.*, 2006) (Bonduriansky *et al*., 2007b). However, Bonduriansky and Day (2003), using an allocation trade-off model, have demonstrated that positive

allometry evolves only under restrict selection conditions, when the net advantage gain of an increase in trait size for individuals of larger size is greater than for individuals of smaller size. Contrarily, a negative allometric relation will evolve when a larger trait size in individuals compensates for a small body size and small individuals start to invest more in the size of the sexual trait (Bonduriansky, 2007b). Contradictions to the traditional view that sexually selected traits always show positive allometry were observed among insects in the legs used as a signal and weapon in drosophilid species (Eberhard, 2002), in the head, antennae and legs used in intrasexual competition in a piophilid fly (Bonduriansky, 2006) and in four species of tephritid flies (Briceño *et al.*, 2005), in the mandible of a species of stag beetles (Pomfret & Knell, 2006), in the forceps of earwings (van Lieshout & Elgar, 2009) and in the postocular flange of a species of dobsonfly (Ramírez-Ponce *et al*., 2017).

Stalk-eyed flies of the predominantly old world family Diopsidae have been used as model organisms in a number of studies on allometry and sexual selection of ornament traits (Baker & Wilkinson, 2001; Cotton *et al*., 2004; Ribak *et al*., 2009; Voje & Hansen 2012). In probably the most comprehensive study of allometry of the stalked-eye flies, Voje & Hansen (2012) reanalyzed the allometric slope of 30 species of diopsids and found the eyestalks positively related to the size of the body in the majority of males of the dimorphic species. *Plagiocephalus*, of the cosmopolitan family Ulidiidae, is another group of stalk-eyed fly, in which the males of the three known species possess eyes on stalks. One of the species of the genus, *P. latifrons*, has extraordinary eyestalks that can reach about five times the size of the body (Grimaldi & Engel, 2005). Males of *P. lobularis* have the smallest eye span in the genus, and *P. intermedius* has an intermediate eye span among the species (Kameneva, 2004). Because of the great intraspecific plasticity and the difference in eyestalks length among the species of the genus, these flies represent excellent models for evolutionary and morphological studies of scaling relationships of sexual dimorphism traits. Thus, the objective of this study is to analyze how eye span is related to variance in body length in two species of *Plagiocephalus*.

Material and methods

To provide a quantification of the sexual dimorphism we measured both males

and females of *Plagiocephalus latifrons* and *P. lobularis*. We obtained morphological measurements from 39 males and 48 females (87 specimens) of *P. latifrons*, and 21 males and 40 females (61 specimens) of *P. lobularis*. The measured specimens were prevenient from the following collections: CEUA (Colección Entomológica, Universidad de Antioquia, Medellín, Colombia), DZUP (Museu de Zoologia Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil), INPA (Instituto Nacional de Pesquisas da Amazônia, Coleção Sistemática de Entomologia, Manaus, Amazonas, Brazil) and USNM (United States National Museum of Natural History, Department of Entomology, Washington, District of Columbia, United States).

We measured the eye length from the median ocellus to the inner edge of the right eye (Fig. 1A). We chose to measure the eye length from the right side of the head to avoid inaccuracy of the angle of eye span. We accessed the measurements of body size by the length of the scutum of the thorax (Fig. 1B). We included as nonsexual control traits the scutellum (Fig. 1B), anepisternum (Fig. 1C) and femur of the fore leg (Fig. 1D). The measurements were taken under a stereomicroscope Zeiss Stemi DV4. Each measure was taken three times in each specimen, and the mean of the three values was used in the analysis to avoid bias. The mean value of the measurements taken from *P. latifrons* and *P. lobularis* are shown in the Table 1. For each measure, the standard deviation was calculated to confirm the reliability of the measurements. The allometric value of the eyestalks was assessed on a log scale by the linear equation $log(y) = log(a)+blog(x)$, in which y is the trait value, x is the body size, a is the intercept and b is the allometric slope. We used a simple linear regression in the software R.

Results

The results demonstrated an almost isometric relationship of all control traits in relation to the size of the body in both sexes of both species (Fig. 2, Tables 2 and 3). The simple linear regression of eye-span plotted against body size of females of *P. latifrons* and *P. lobularis* exhibited an almost equal isometric relation (b = 1.15 and b = 0.98, respectively) and intercept values (a = -1.25 and a = -1.23, respectively) (Fig. 2, Tables 2 and 3). The results also showed a steep and nearly identical allometric slope between

males of *P. latifrons* (b = 3.14) and *P. lobularis* (b = 3.15), but higher intercept in *P. latifrons* (a = -0.03) than in *P. lobularis* (a = -1.34) (Fig. 2, Tables 2 and 3).

Discussion

Bonduriansky and Day (2003) suggested that isometry is selected when fitness is an increasing function of the trait size alone. Because larger-bodied individuals have more energy to spend on trait growth, it is advantageous to invest in body growth as well. When all body sizes invest equally in body growth and trait grown, an isometric relation is resulting (Bonduriansky & Day, 2003). However, a perfect isometric relation is an exceptional case (Gould, 1966), and the majority of traits in most organisms appear to scale negatively with body size (Eberhard, 2002). We found that the eye length of females and the control traits (length and width of scutellum, anepisternum height and leg length) scaled isometrically with the body size of both species, with some values very close or perfectly isometric (Tables 2 and 3). We did not find any significant negative allometry from our results. The lowest allometric value found was 0.70 for the length of the scutellum of females of *Plagiocephalus latifrons*.

On the other hand, the allometric slopes registered for males of *P. latifrons* and *P. lobularis* were, respectively, 3.14 and 3.15, the steepest positive values for stalk-eyed flies that have been recorded. Voje and Hansen (2012) encountered an allometric slope of 2.69 for *Diasemopsis longipedunculata*, the highest exponent among the 30 diopsids species analyzed in their work. Although we are comparing the allometric slope of two taxa of stalk-eyed flies, the eyestalks in Diopsidae and *Plagiocephalus* evolved from different mechanisms and it is unknown whether they have the same growth regulation (Grimaldi & Engel, 2005). In another study, Kodric-Brown et al. (2006) analyzed the allometric exponent of sexually selected traits in nine major taxa, including vertebrates, such as lizards and deer, and invertebrates, such as beetles and crabs. The authors found the allometric scaling exponents within species usually ranging from 1.5 to 2.5, with few cases presenting exponents above 3. This illustrates that the allometric slopes of the sexual secondary trait of *Plagiocephalus* are also among the highest found in animals.

Male individuals of *P. latifrons* and *P. lobularis* have a highly contrasting mean of stalked eyes length and an almost equal mean of body length (estimated by the scutum

length) (Table 1). However, we found between these two closely related species a nearly equal allometric slope. So contrarily as expected, the difference in trait size between the species did not result from changes in body size, and variation in the size of eyestalks did not cause divergence in the allometric slope between the species. In studies on diopsids, the extreme size of the eyestalks of some species was explained by differences in the size of the body, and differences in static allometric slopes were predicted by the relative size of the eyestalks (Voje & Hansen, 2012; Voje *et al*., 2013). In our study, we found that the difference in the mean of trait size in relation to body size in *Plagiocephalus* has arisen through changes in the intercept (Tables 2 and 3). This result shows that trait size is not always directly influenced by the size of the body and that the intercept is more evolvable than the slope in some cases, as pointed out for genital traits (Eberhard *et al*., 1998; Voje *et al*., 2003).

Allometric slopes among closely related species usually vary very little, reflecting the idea that allometric relationships are constrained by biological mechanisms (Pélabon *et al*., 2014). In a survey made by Voje et al. (2013), it was observed that the static allometric slope varied more across species than in a subspecies level, meaning that allometric exponents are difficult to change in short timescales. The idea that static allometric slope has low evolvability and is constrained on microevolutionary scales could be applied to our results. The same pattern of positive allometric slope observed between these two closely related species could suggest a recent influence of a strong sexual selection in the evolution of the eyestalks in this genus of stalk-eyed fly.

Several authors have demonstrated that the expression of secondary sexual traits, such as the eyestalks in flies, is conditioning dependent (Bonduriansky, 2007a; Bonduriansky & Rowe, 2005). The trade-off between allocating sources and mating success is evidenced by the high variation in the size of this sexual secondary character in the individuals of some stalk-eyed species. We did not observe a decline in the slope towards the ends of the allometric curves, as seen in lucanids (Coleoptera) and referred as an increase in costs that were constrained by resources (Emlen & Nijhout, 2000).

This study reveals a positive and equally steep allometry in the eyestalks of males of both species of *Plagiocephalus* analyzed in this work. We could conclude from this study that sexually selected trait size is not always directly influenced by the size of the

body and that the intercept may be subject of more variation during evolution than the allometric slope. From these results, we can address some questions for future research. Why closely related species that present the same mean of body size can present so divergent mean of trait size? What drives this difference if the individuals of same body size would have the same amount of sources to spend on the trait? Why there are cases in which the allometric slope of closely related species with similar body size and contrasting trait size is equal and sometimes it is not? Is the force of sexual selection reflected in the allometric slope or in the size of the sexually selected trait?

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Table 1 Mean value of the measurements taken from *Plagiocephalus latifrons* and *Plagiocephalus lobularis*.

Species		Measurements					
		Eyestalk	Scutum	Scutellum width	Scutellum length	Anepisternum	Femur
P. latifrons							
	Male	4.836	1.671	0.474	0.809	0.728	1.712
	Female	0.520	1.913	0.560	0.973	0.780	1.520
P. lobularis							
	Male	1.306	1.650	0.521	0.835	0.775	1.555
	Female	0.470	1.633	0.460	0.753	0.700	1.293

Table 2 Values of allometric slope and intercept for males and females of *Plagiocephalus latifrons* according to each body trait in function of body size. LC = lower coefficient; UC = upper coefficient.

	P. latifrons						
		Slope	Intercept	LC Slope	UC Slope	LC Intercept	UC Intercept
Eye length	Male	3.14	-0.03	2.75	3.52	-0.23	0.16
	Female	1.15	-1.25	0.88	1.43	-1.43	-1.08
Scutellum length	Male	1.01	-1.26	0.77	1.25	-1.39	-1.14
	Female	0.70	-1.02	0.46	0.94	-1.18	-0.87
Scutellum width	Male	1.04	-0.75	0.91	1.17	-0.81	-0.68
	Female	0.91	-0.65	0.72	1.10	-0.77	-0.52
Anepisternum height	Male	0.94	-0.80	0.79	1.10	-0.88	-0.72
	Female	0.97	-0.83	0.79	1.14	-0.95	-0.72
Femur length	Male	1.16	-0.06	1.04	1.28	-0.12	0.00
	Female	1.12	-0.24	0.93	1.31	-0.36	-0.12

Table 3 Values of allometric slope and intercept for males and females of *Plagiocephalus lobularis* according to each body trait in function of body size. LC = lower coefficient; UC = upper coefficient.

	P. lobularis						
		Slope	Intercept	LC Slope	UC Slope	LC Intercept	UC Intercept
Eye length	Male	3.15	-1.34	2.63	3.66	-1.60	-1.08
	Female	0.98	-1.23	0.85	1.12	-1.32	-1.15
Scutellum length	Male	0.89	-1.10	0.70	1.08	-1.19	-1.00
	Female	0.85	-1.10	0.70	1.01	-1.20	-1.01
Scutellum width	Male	1.00	-0.68	0.81	1.19	-0.78	-0.58
	Female	0.93	-0.66	0.81	1.05	-0.73	-0.58
Anepisternum height	Male	0.90	-0.70	0.70	1.09	-0.80	-0.61
	Female	1.01	-0.83	0.89	1.12	-0.90	-0.76
Femur length	Male	1.01	-0.07	0.87	1.16	-0.14	0.00
	Female	0.93	-0.18	0.79	1.07	-0.27	-0.09

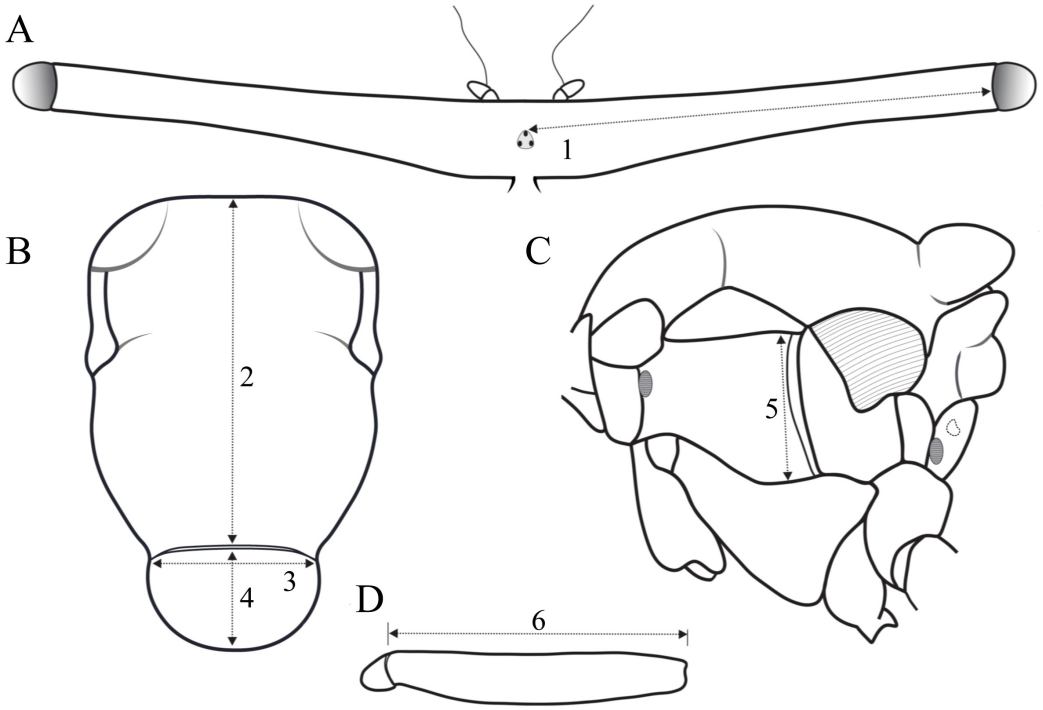

Figure 1. Schematic illustrations of the body parts where morphological measurements were taken. Male of *Plagiocephalus latifrons*: A. Dorsal view of the head: 1 = length of the eye; B. Dorsal view of the thorax: 2 = length of the scutum (corresponding to the body size), 3 = length of the scutellum, 4 = width of the scutellum; C. Lateral view of the thorax: 5 = height of the anepisternum; D: Lateral view of the anterior femur: 6 = length of the anterior femur.

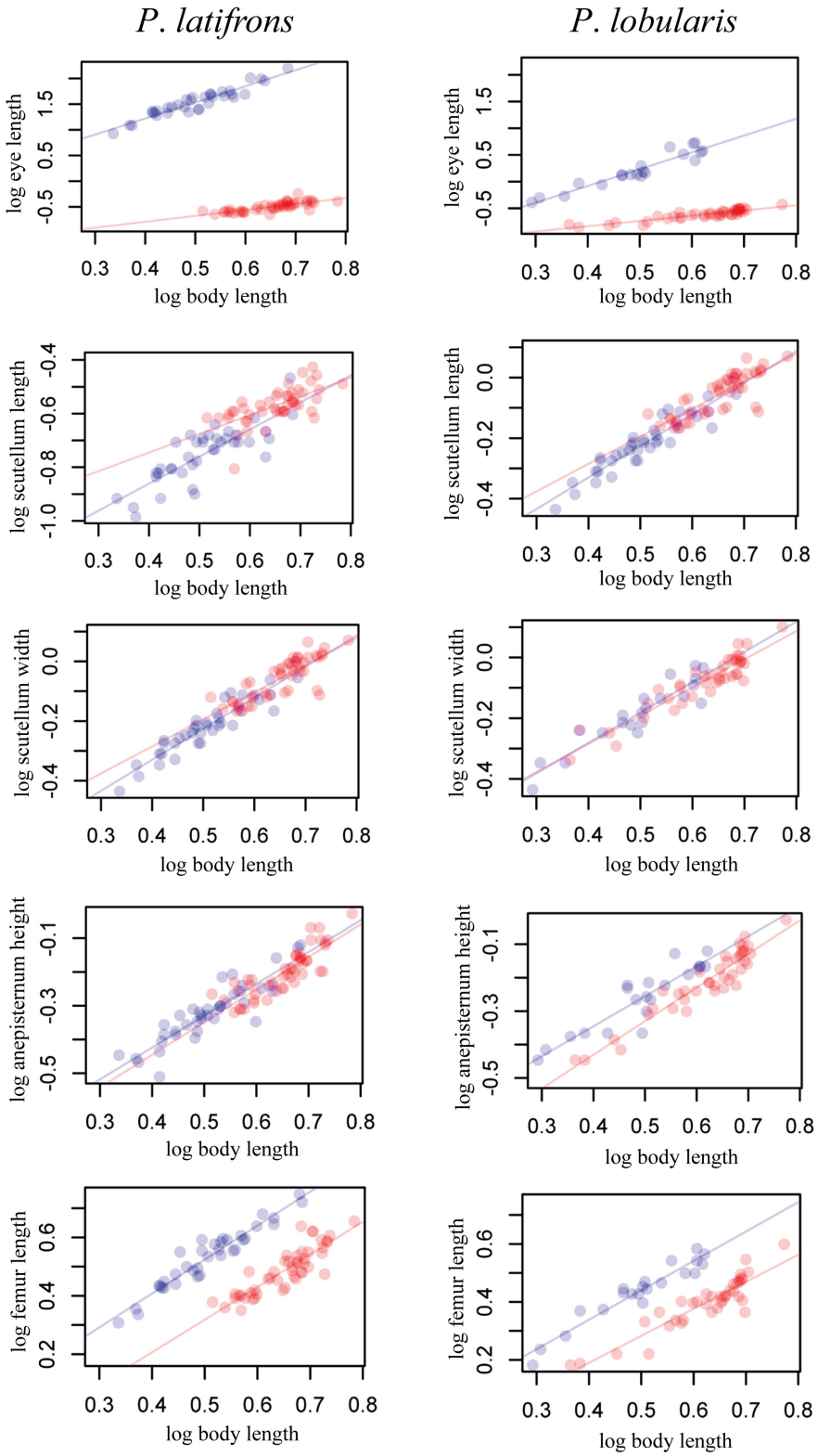

Figure 2. Simple linear regression of the size of five morphological measurements plotted against body size. All data are log-transformed. Males are shown as blue circles and females are shown as red circles.